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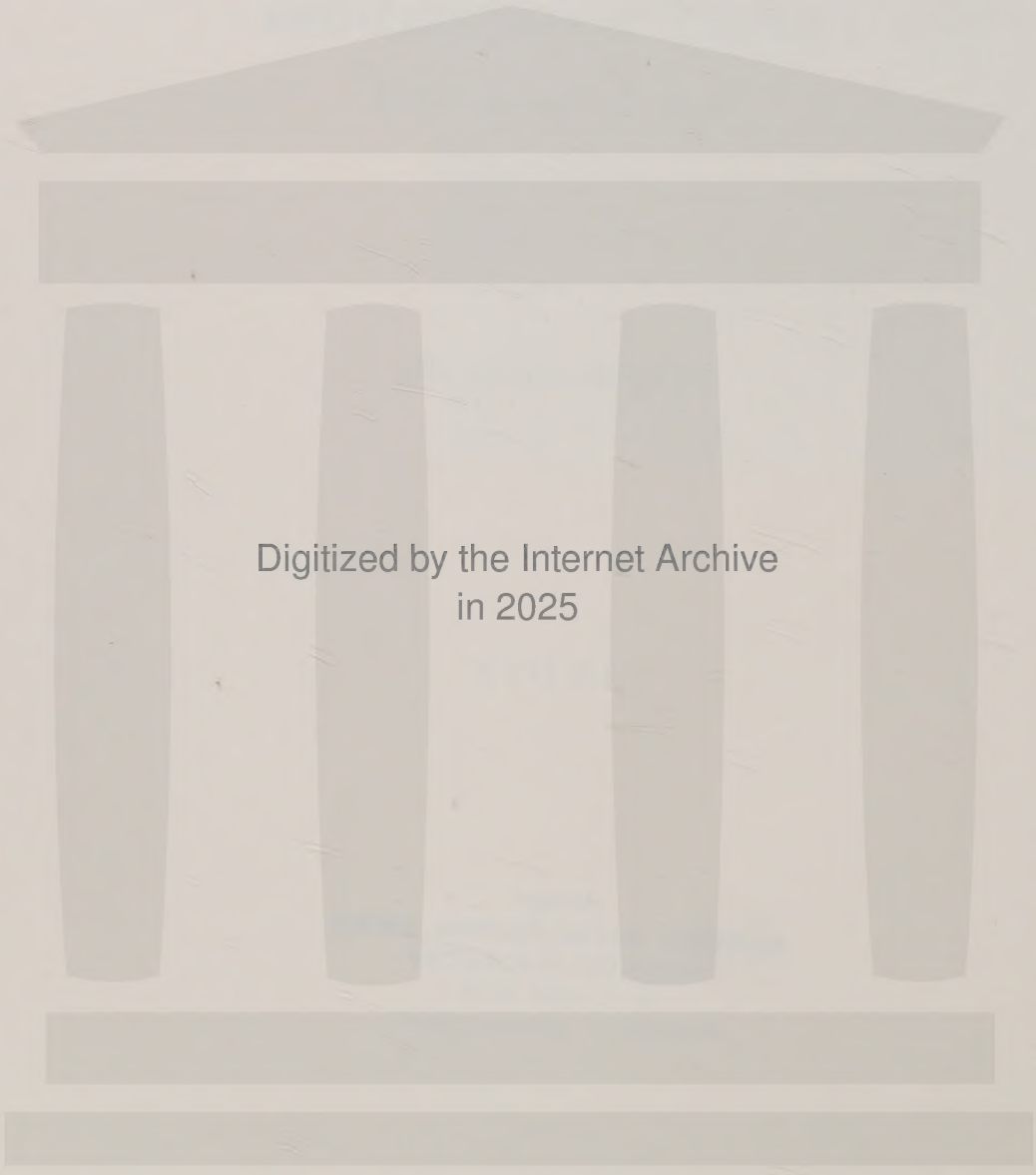

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MINISTRY OF AGRICULTURE, FISHERIES AND FOOD

FISHERY INVESTIGATIONS

Series II, Volume XXVI, Number 1

The laboratory culture of the prawn *Palaemon serratus*

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LONDON HER MAJESTY'S STATIONERY OFFICE 1969

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ABSTRACT

The spatial and temporal distribution and abundance of the prawn *Palaemon serratus* are discussed, together with the method of transport of live animals from the port of landing to this laboratory. Spawning and the period of egg-carriage are related to temperature, and the techniques of obtaining larvae are indicated and related to estimations of fecundity. Moulting in laboratory populations of wild animals was shown to be rarely accompanied by growth, nor was moulting frequency related to size in adults. Methods of reducing cannibalism in soft newly-moulted prawns are discussed, and other causes of mortality in laboratory populations noted. The relationship between wet and dry weight and total length for adults is given, and oxygen consumption and ammonia production were measured. Specimen calculations are made to illustrate the applicability of the latter figures in estimating optimum tank sizes and water circulation rates. Prawns were found to be able to regulate oxygen consumption down to 50 per cent saturation, and to have a Q_{10} value of only 1.2 between 12 and 17°C. Their tolerance to ammonia in the external medium was found to be high.

Rearing prawn larvae in unfiltered water and in darkness adversely affected survival, as did the provision of water turbulence by bubbling. The optimum temperature range for growth, survival and metamorphosis was 20–25°C, although there were considerable variations between broods. The optimum salinity was that of normal sea water, although it was found that a wide range of tolerance existed. Density and survival of larvae were inversely related, and methods of estimating the effects of cannibalism are discussed. A theoretical maximum survival rate to metamorphosis was put at 90 per cent. Of the various foods tested, only *Artemia* nauplii proved adequate for prawn larvae. The relationship between food concentration and larval growth rate was studied. The suitability of mussel meat for older animals was suggested. Variations in the food value of different stocks of *Artemia* were demonstrated and the implications are discussed. Long-term rearing of both *Palaemon serratus* and *P. elegans* indicated that growth could be doubled compared with that in the natural environment. The implications of these results for large-scale rearing are discussed and compared with other studies from the literature.

Figure 1 Sketchmap to show the distribution (thickened line) of *Palaemon serratus* around the coast-line of Europe.

The laboratory culture of the prawn
Palaemon serratus

INTRODUCTION

GENERAL

Intensive experimental studies into the possibilities of the culture of marine food organisms in the United Kingdom began about 1950 with the work of Walne on oysters (Walne 1956, 1964, 1966), and later that of Shelbourne on plaice (Shelbourne, Riley and Thacker 1963). Other species of invertebrates have subsequently received attention at Conway. These include the English prawn *Palaemon serratus*, and the American hard-shelled clam *Mercenaria mercenaria*. For a short history of marine fish hatcheries, see Shelbourne *et al.* (1963).

In many tropical countries, especially those bordering the Indo-Pacific region, shrimp and prawn farming has been pursued for a very long time. The method typically entails the flooding of shallow ponds or paddy-fields with sea water at times of the year when large numbers of prawn larvae and post-larvae are occurring naturally in the water. By provision of a plentiful food supply and control of potential predators, the young prawns or shrimps are encouraged to grow to a marketable size in only a few months, at which time they are harvested (see, e.g., Gopinath 1956).

The terms 'shrimp' and 'prawn' are used throughout the literature as common names. There is no universally accepted relationship between these terms and the taxonomic affinities of the animals under consideration. The term 'prawn', however, usually indicates a species of the family Palaemonidae (*Palaemon*, *Macrobrachium*), and 'shrimp' refers to members of the family Penaeidae (*Penaeus*). *Crangon vulgaris*, the English brown shrimp, is one of several exceptions.

As far as can be ascertained, the only commercial operation in which freshwater or marine prawns or shrimps are reared from the egg under controlled conditions involves the shrimp *Penaeus japonicus* in Japan (Hudinaga and Miyamura 1962; Fujinaga 1963; Idyll 1965; see also Hudinaga 1942). In this operation, the egg-bearing females are captured and held until the brood of several hundred thousand eggs has been shed. The resulting nauplii are separated and fed on algae, which are later supplemented with *Artemia* (the brine shrimp). The post-larvae are eventually transferred to outside ponds to fatten during the summer. In Malaysia, the freshwater prawn *Macrobrachium rosenbergi* has been successfully cultured on a laboratory scale from egg to adult (Ling and Merican 1961; Ling 1962). *Macrobrachium*, which has a fecundity comparable to that of *Penaeus japonicus*, requires only 9 months to reach a weight of 100 g.

In the United States, where the penaeid shrimps form the most valuable commercial fishery, interest has developed in the possibilities of shrimp farming (Allen 1963). Attempts have been made to rear naturally-occurring post-larvae in ponds, with some success (Lunz 1956; 1964). Scientists of the U.S. Bureau of Commercial Fisheries at Galveston are engaged in laboratory investigations (Zein-Eldin 1963, Zein-Eldin and Griffith 1966), and some work has been done on the artificial cultivation of *Macrobrachium* (Ingle and Eldred 1960). More recently, at the Institute of Marine Sciences of the University of Miami, a study has begun of the feasibility of pond culture of penaeids in connection with a newly-constructed power plant on the shores of Biscayne Bay. Also, larval lobsters have been reared to the fourth stage and released into the sea routinely over more than 10 years (Hughes and Matthiessen 1962). There is much earlier work on lobster rearing, both in Europe and America, but it is not necessary to review this here.

There exists a large body of literature concerning the laboratory rearing of larval crustaceans, but this refers almost entirely to the description of larval stages reared under standard conditions, from which drawings have been made for the purposes of identification. There are very few papers concerned primarily with rates of growth and survival, apart from those mentioned above. Initial studies on the larvae of the

commercially important *Penaeus aztecus* of the U.S.A. were reported in Contribution No. 207 of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas, in which temperature and growth rate were shown to be directly related. Ewald (1965) has demonstrated that *Penaeus duorarum*, another commercial shrimp from the same region, can also be reared through all its larval and post-larval stages under suitable conditions. Studies of certain specific factors affecting decapod larvae were undertaken by (among others) Templeman (1936) on lobsters, by Sandoz and Rogers (1944) on *Callinectes*, by Broad (1957) on *Palaemonetes*, by Coffin (1958) on *Pagurus*, by Costlow, Bookhout and Monroe (1960) on *Sesarma*, and by Bookhout (1964) on *Pagurus*. Most of these were concerned with the effects of temperature and salinity only.

Palaemon serratus was formerly known as *Leander serratus* (see Holthuis 1950, for history of synonyms). Keys for the purposes of identification of the species of this genus are provided by Holthuis and also by Kemp (1910). *P. serratus* was chosen for the initial studies in the present experiments, since it is the largest species available in Britain, is commercially valuable, and, being an inshore animal, was considered likely to possess greater hardiness under laboratory conditions than, for instance, the deeper-water *Pandalus borealis*. It has been used extensively in laboratory studies of chromatophores, moulting control, salt and water balance, nerve conduction and other phenomena (see Waterman, ed., 1960). Its life history and ecology were the subject of papers by Gurney (1923), Forster (1951a) and Cole (1958), for populations around the coasts of southern England and North Wales. Studies of the development of the larva have been made by Gurney (1924) on specimens from the plankton and by Sollaud (1923) from laboratory-reared animals.

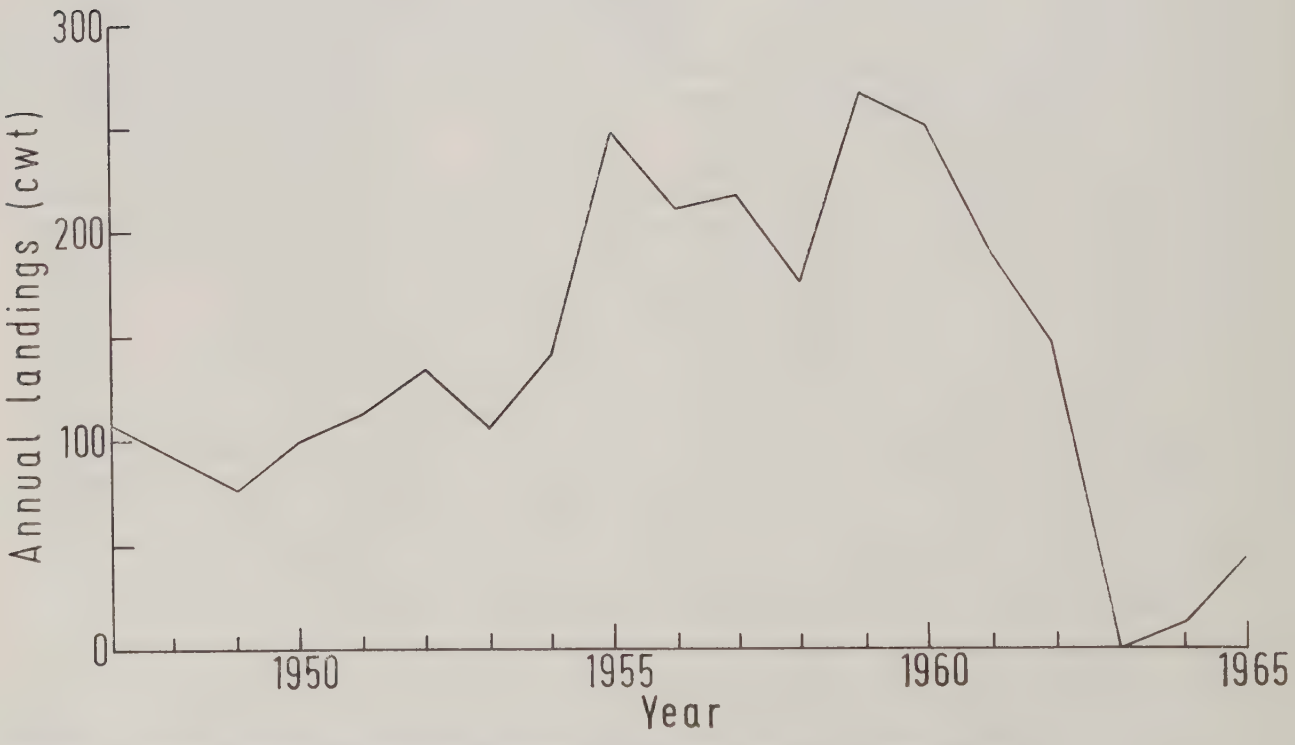


Figure 2 Annual landings of *Palaemon serratus* at English ports from 1947 to 1965.

DISTRIBUTION AND ABUNDANCE

Palaemon serratus is a Mediterranean species which extends around the west coast of France and northwards for some distance (Figure 1). Gurney (1923) noted its occurrence around the shores of France, Italy, Greece and the Bosphorus, and Algeria. It is not uncommon as far north as Holland (Holthuis 1950) and has been recorded from Denmark. It is common around the coasts of the British Isles up to a line extending from the Clyde to the Wash, and including most of Ireland.

The only United Kingdom fishery for this species is carried out along the south coast of England from Sussex to Cornwall. According to Ministry of Agriculture, Fisheries and Food fisheries statistics, there was a gradual increase in the annual catch, from 100 cwt in 1947 to 200 cwt in 1962 (Figure 2). Following the harsh winter and consequent very low sea temperatures early in 1963, no prawn landings whatsoever were recorded for that year; in 1964 and 1965, totals of 11 and 42 cwt respectively indicated a slow recovery, which has continued.

Prawns are fished mainly with the aid of pots, which may be either converted from lobster pots or specially designed cubical traps with about 15 inch sides (Ministry of Agriculture, Fisheries and Food, Laboratory Leaflet No. 10, 1956). Some fishing is also done by means of a beam trawl. Several grounds fished prior to 1963 have since been neglected, possibly because former fishermen have sought alternative and more stable employment. This factor, combined with the tendency of the men to restrict their fishing since 1963 to the period between October and March, made it very difficult to obtain regular supplies of experimental animals throughout the year.

COLLECTION

Although the laboratory undertook fishing expeditions of its own around the North Wales coast from 1964–66, only rarely were significant quantities of prawns found. For obtaining numbers in the order of 500–1 500 arrangements were made for the purchase of live animals from south coast fishermen at the quayside. The prawns were separated into large polythene bins which contained sea water brought from Conway, because south-coast quayside water was often heavily contaminated with oil. The bins were lidded, and contained baffles in the form of oyster spat collectors (Walne 1966) which reduced splashing to a minimum; they also enabled the prawns to make full use of the available volume by spacing themselves around the collectors, instead of congregating in a dense mass on the container bottom. During the journey to Conway, which took 10 hours or more, oxygen from a cylinder was bubbled through the water.

Mortality during transport usually varied between 5 and 10 per cent, although part of this must be attributed to the fact that prawns were often stored in keep-pots by the fishermen, and might have been in captivity for several days before collection. On one occasion, when the air temperature fell below 0°C, about one-third of the animals died in transit; their inability to withstand temperatures below 3–4°C was subsequently confirmed by experiment.

From 1964 to 1966 prawns were collected from the south coast at irregular intervals between the months of October and March. During the winter months the percentage of berried females (i.e. those carrying eggs) in the total catch of males and females increased, reaching over 60 per cent in March, when commercial fishing stopped.

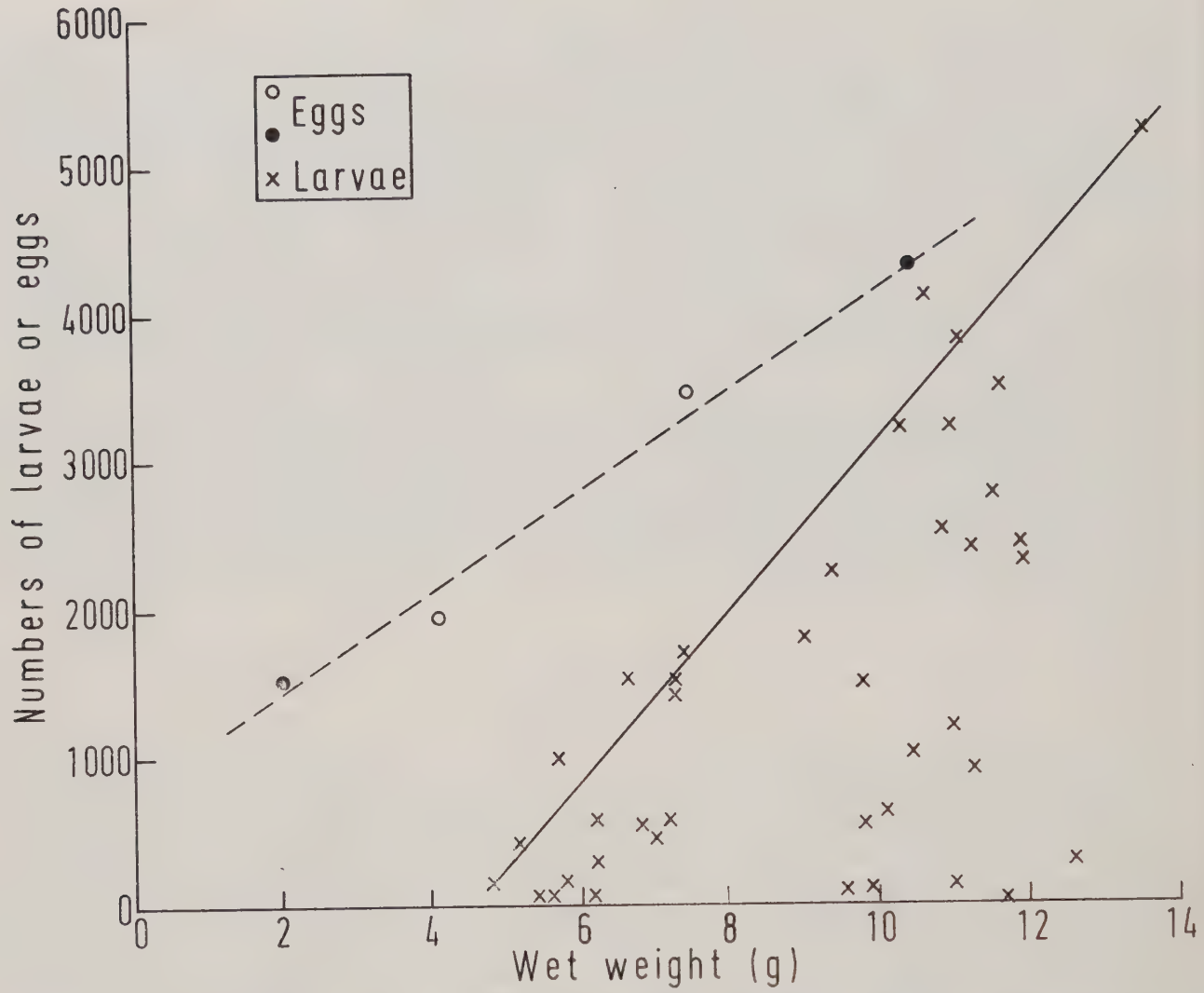


Figure 3 The relationship between the number of eggs and of larvae produced and the wet weight of the female in *Palaemon serratus*. The solid line in the figure indicates the approximate maximum number of larvae recovered from a female of any given size. Solid circles indicate egg observations derived from the data of Forster (1951a); open circles indicate those of the present study.

MAINTENANCE OF LABORATORY STOCK

BREEDING STOCK

Stock prawns were held both inside and outside the laboratory in tanks where the water temperature was approximately the same as that from which the animals had originally been taken. Some of the berried females were gradually warmed to 20°C in order to decrease the period of egg carriage. It is clear from the review of field data by Cole (1958) that the length of time of egg incubation and the temperature of the surrounding water are directly related. It was possible to obtain an indication of this relationship in the laboratory, on occasions when prawns with mature gonads spawned successfully in the tanks and came into berry. About ten such newly-berried animals were held separately in containers at each of three different temperatures (10, 15 and 20°C). The mean time of egg carriage at 20°C was 28 days, and at 15°C was 58 days. An accident curtailed the 10°C experiment after 95 days, by which time the embryos were showing eye spots, a sign of advanced development.

Tank populations of berried females which were being warmed to accelerate hatching were inspected individually twice weekly. Eggs which were within a few days of hatching were recognizable by (in addition to the possession of eye spots) their loss of colour, and in the very advanced stages by distortion from the spherical shape, and even by rhythmic internal movements. Females whose eggs showed any of these characteristics were placed in tanks darkened except for the area around the outflow pipe. On hatching, larvae were attracted to the outflow by the light and collected in a second tank. On occasions when larvae from a single brood were required unmixed with others, individual berried females were kept in one-litre beakers until their larvae hatched.

Almost invariably hatching took place at night; a female which had hatched only part of her eggs by the morning rarely produced more during daylight hours, but the following night a further crop of several hundred larvae would appear. A typical set of figures for a total hatching from a berried female over a night/day/night period was 980/0/2475.

The fecundity of *Palaemon*, in terms of numbers of eggs carried in relation to the total length of the prawn, was reported to extend from about 1 500 to 4 300 for animals ranging from 6.2 to 10.5 cm in length (Forster 1951a). In the present work, fecundity was measured as the number of viable larvae removable from a vessel in which a berried female had completed her hatching. In Figure 3 the results of these counts are shown as a function of the wet weight of the animal (unberried). The solid line in the figure indicates the approximate maximum number of larvae recovered from a female of any given size. Many females yielded numbers of larvae far fewer than might be expected, which suggested that they might be consuming some of their offspring before the latter could be separated from them. Tests in which known numbers of newly-hatched larvae were added to vessels containing recently-berried female prawns showed that after 24 hours up to 90 per cent of the larvae might be consumed. The maximum hatching rate of Figure 3 might reasonably be expected to have occurred when no cannibalism was taking place, yet it is considerably below that expected on the basis of the figures of Forster (1951a) for egg-bearing which are plotted as solid circles. Forster's figures were confirmed by counting the dried eggs from three small and three large berried females, and the averages for the two sizes are shown as open circles in Figure 3. It is seen that both my observations and those of Forster fall close to the same straight (broken) line, thus confirming that maximum larval production was somewhat lower than the number of eggs normally carried.

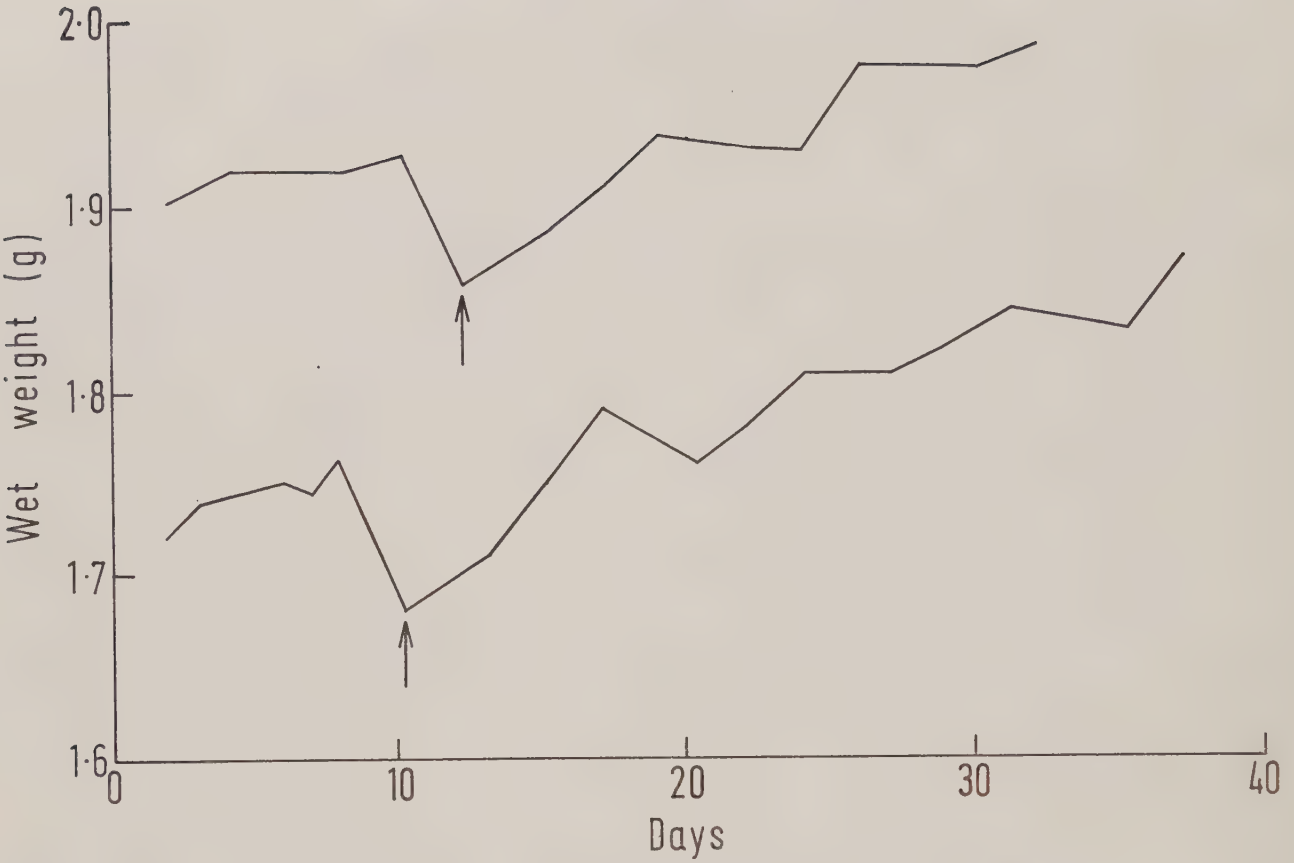


Figure 4 The change in weight of two prawns over a period including a moult. The arrows indicate the day of moulting.

MOULTING

Experiments were conducted to investigate the frequency of moulting in prawn populations in the warm water of the laboratory. The susceptibility of soft newly-moulted animals to attack from others of the same species has often been noted (e.g. Jefferies 1964). It would therefore be expected that animals which are held in crowded laboratory tanks at high temperatures would moult and be exposed with a soft cuticle more frequently, and consequently be more often liable to attack, than in their natural environment.

In the first experiments, in order to avoid the effect of cannibalism, the prawns were kept isolated from each other by means of rigid mesh plastic spacers. However, this method proved unsatisfactory, because on moulting the animals trapped their soft appendages and rostrum in the mesh, damaging or breaking them off in an effort to escape. Moreover, the original intention of allowing a small degree of physical contact between prawns was thus frustrated. In a subsequent experiment the animals were therefore confined individually in one-litre beakers, to which fresh mussel tissue was added for a few hours each day as food. The water, maintained at 20°C and continuously aerated, was changed daily, immediately after removing the surplus uneaten food. Animals ranging from 5 to 9 cm in total length were wet-weighed initially and three days after each moult; the exuvium was also dried and weighed. The experiment was continued for 62 days during the months of July and August. The average weekly death rate was 7 per cent and dead animals were replaced. A total of 45 prawns passed through two moults, 15 through three, and 2 through four moults; although some gained weight steadily, some became smaller, and there was no overall mean weight change over three moults (1.74 to 1.66 g wet weight). Some animals were weighed more frequently, and two examples of those which showed a weight increase are recorded in Figure 4. In these two examples there was a steady increase in weight throughout the intermoult period, and on the day of moulting there was a large drop in weight which could be correlated with the loss of the exuvium.

Although it might be expected that there would be a positive correlation between the duration of the intermoult period and the size of the prawn, no evidence was found for this in animals ranging in wet weight from 1.2 to 6.2 g. The mean duration of the intermoult period for these adults was 21 days. In an experiment in which tank populations were maintained at temperatures of 20 and 12°C, the mean durations of the intermoult period were 14 and 24 days respectively; these animals had been taken from the sea in February, and those which were kept at 20°C may have been stimulated to moult faster than normal by the rapid warming which they experienced.

The weights of the exuvia of these adult prawns were obtained and found to be 4.5–6.5 per cent of the total wet weights of the animals. In each case the prawn was weighed three days after moulting; the exuvia were oven dried at 80°C before weighing. A consistent exuvium wet weight could not be obtained, because it was impossible to remove completely the excess water clinging inside the hollow skeleton.

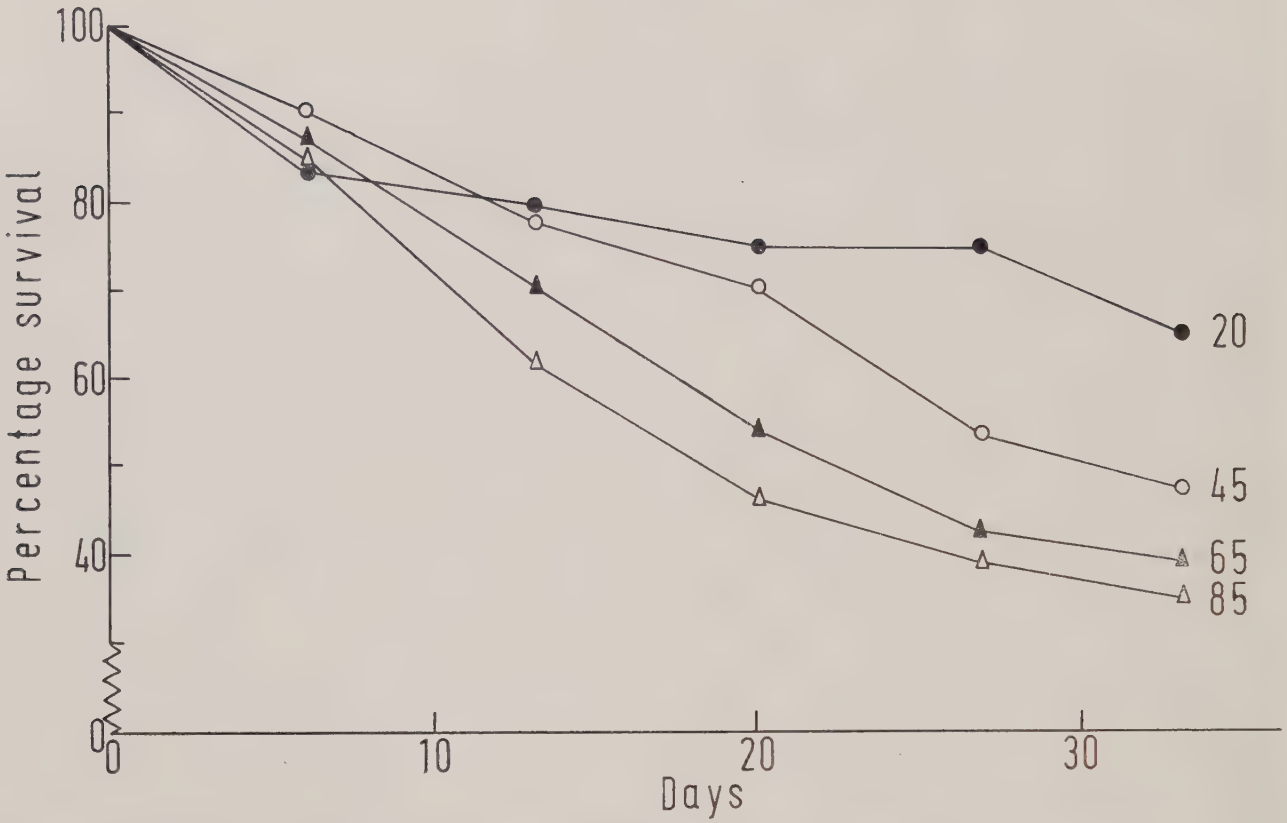


Figure 5 The effect of various initial population densities (20, 45, 65 and 85 prawns per 50 litres) on survival.

MORTALITY IN STOCK TANKS

The frequent deaths of soft prawns in laboratory tank populations gave an early indication that some form of protection for soft animals was essential. The simple expedient of reducing the density of the population had a clear effect on survival. Figure 5 shows the percentage survival for four experiments in which there were initially 85, 65, 45 and 20 prawns in 50-litre tanks. These data, which were provided by my colleague John Forster, indicate a higher rate of survival at lower densities. Attempts to provide 'hides' for moulting prawns have so far produced inconclusive results. These hides ranged from stones, seaweed, brushwood and tunnels drilled in masonry to dark areas provided by opaque rigid polythene.

It is certain that the survival of laboratory populations is influenced by other factors, one of which is microbial infection. Prawns were occasionally found to develop small brown spots over their entire cuticle, which on microscopic examination appeared to be pits where the cuticle had been destroyed. This appearance was not inconsistent with the disease in lobsters caused by chitiniverous bacteria (Hess 1937). Non-infected prawns became infected, in contrast to control groups, when infected prawns were placed amongst them; at 20°C, it required about two weeks for initially 'clean' animals to show many brown spots. They usually died a few days later.

A further manifestation in prawns which always subsequently died was an effect known as 'white spot'. In this case the posterior part of the abdomen became an opaque dull white, which quickly spread towards the anterior end, and was followed rapidly by a pink tinge, a sign of decomposition of the tissues. These symptoms also appeared to spread rapidly through a population. These two phenomena of 'brown spot' and 'white spot' leading to death in prawns were noted by Edwards (personal communication) at the Burnham-on-Crouch laboratory of the Ministry in 1960–61. Enquiries of fishermen indicated that the symptoms described above are not seen in freshly-caught prawns.

Other visible effects of infection have been encountered, although they have not been seen to spread in laboratory populations. In every 1 000 prawns from the south coast of England, about two animals carried the crustacean parasite *Bopyrus:* North Wales prawns were never found in this condition, a fact also noted by Cole (1958). Another rare condition in prawns from the field occurred when the entire body was a dense chalky white. Unlike the white spot effect mentioned above, animals would live in this condition for several weeks and remain active. G. R. Forster (personal communication) has also encountered such a phenomenon, and has found these prawns to be infected with a sporozoan parasite *Telohania*, which has also been reported in penaeid shrimps (Hutton *et al.* 1959). A further infection found in only two animals which were taken at the same time bore a close resemblance to the copepod parasite *Nectonema*, reported by Nouvel-van-Rysselberge (1937) in prawns off Roscoff. These prawns were accidentally killed through lack of aeration, rendering positive identification of the parasite impossible.

The causes of a certain proportion of deaths in laboratory populations of prawns could not be identified; these often occurred just before moulting, as determined by the fact that it was possible to pull off the rostrum and find a soft new rostrum beneath. It is possible that these deaths might have been due to dietary deficiencies. In different experiments a variety of foods were offered to the animals, including seaweed, chopped cod, haddock, liver, steak, boiled egg white, commercial fish flakes, and boiled and fresh mussel. Only fresh mussel was taken in substantial quantities, and for this reason prawns were usually maintained on this food, although it is possible that their dietary requirements were not entirely satisfied by it.

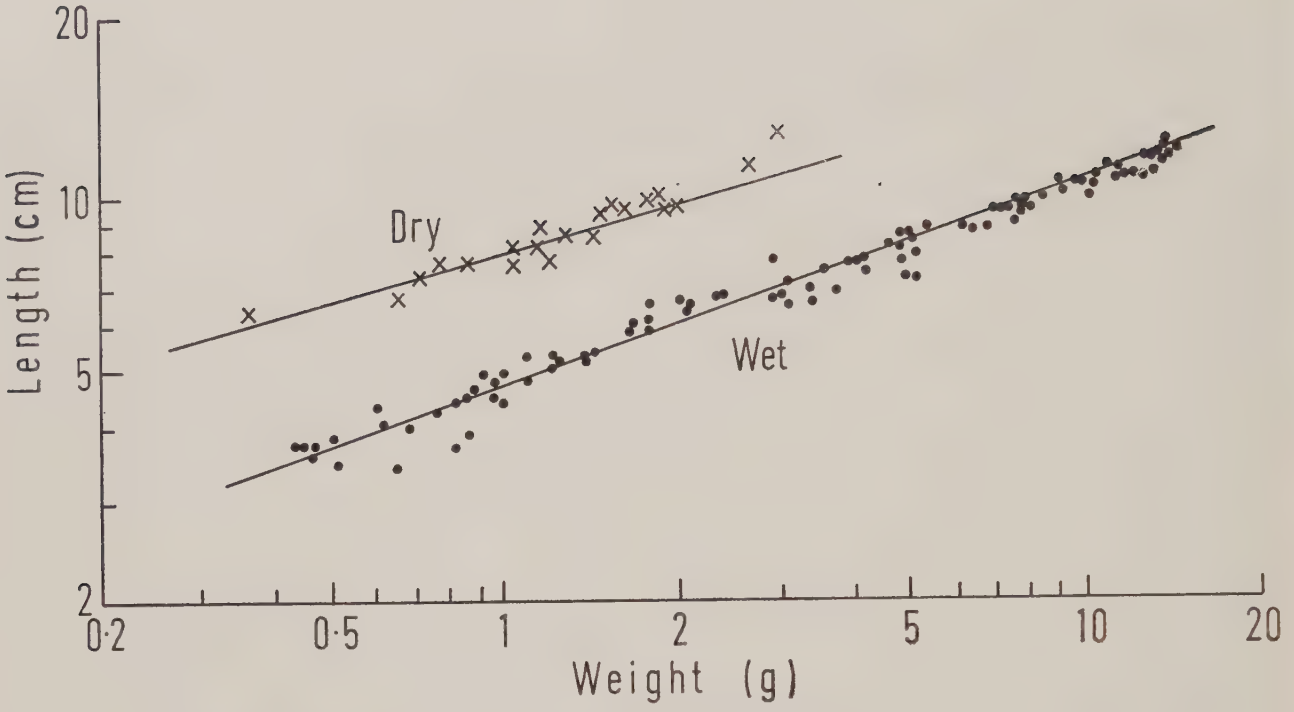


Figure 6 The relationship between total length and wet and dry weights in *Palaemon serratus*. The straight lines were fitted statistically.

LENGTH AND WET AND DRY WEIGHTS

During the course of the various studies associated with this work, information has been obtained (which does not appear elsewhere) regarding the relationship between total length*, wet weight (dried on paper tissues) and dry weight (to constant weight at 80°C). This information is presented in Figure 6; when logarithmic co-ordinates are used the relationships approximate to straight lines, whose regression equations are:

Wet weight $\log y = 0.678 + 0.349 \log x$

Dry weight $\log y = 0.908 + 0.266 \log x$

where x is the weight in g and y is the length in cm. The correlation coefficients were 0.98 and 0.94 for wet and dry weights respectively. Dry weight was approximately 25 per cent of wet weight. Most prawns appeared to be able to withstand drying with paper tissue and exposure in air for several minutes, with the exception of newly-moulted soft animals, which were easily damaged by handling.

* The method of measuring total length was that used by Forster (1951a) which was as follows: 'Tip of the rostrum to the base of the spines on the telson, measured with dividers while the animal rested in its normal upright position on a glass plate'. The prawns were measured fresh because of the curvature of the abdomen that occurs in most preserved specimens.

OXYGEN CONSUMPTION AND AMMONIA PRODUCTION

Oxygen consumption and ammonia production were investigated to gain a basic understanding of the biology of the prawn, and also in order to be able to calculate the optimum tank sizes, flow rates and aeration requirements at a variety of different water temperatures in possible future large-scale operations.

Individual prawns were held in glass-stoppered bottles of water which ranged in capacity from 250–1 000 ml, at standard temperatures of 7, 12, 17 and 22°C, for times ranging from 3–7 hours. About twenty-five different determinations were made at each temperature, using animals ranging in size from 0.5 to 10 g wet weight. At the conclusion of an experimental period, the oxygen concentration of the water in the vessel was determined and compared with that of a control bottle containing no prawns, using an oxygen sensor electrode and associated meter. A 50 ml sample of the liquid was then set aside in order that an ammonia determination could be made upon it within the next few minutes. This was done according to the Nesslerization technique of Wattenberg as described in Barnes (1959), using a spectrophotometer at 400mμ. With a 1 cm cell, transmittancy readings down to 75 per cent were readily obtained, using the original filtered sea water as a blank; over this range the calibration curve was a straight line. This technique usually prevented the development of the turbidities mentioned by Barnes.

The resultant curves for the uptake of oxygen and the production of ammonia are presented in Figures 7 and 8 respectively; on double logarithmic co-ordinates the curves approximate to straight lines, whose regression equations and correlation coefficients are also shown. From Figures 7 and 8 is derived Figure 9, which illustrates the effect of temperature on respiration and ammonia excretion; a standard animal of 5 g wet weight has been postulated for this purpose. The resultant curve for oxygen indicates that over the range 12–17°C there was no direct relationship with temperature; above this temperature range respiration increased, and below this range it decreased. The ammonia data do not show this effect, and ammonia production is directly related to temperature over the whole range.

Figure 10 shows the extent of the regulatory ability of *Palaemon* with regard to its respiration over the range of oxygen tensions up to saturation. The experiment was performed over a period of 4 hours, using a single animal weighing 5 g, in a vessel containing an electrode for the continuous measurement of oxygen concentration. It would appear that below 50 per cent saturation (3 ml/l) the regulatory ability fails. It is possible that the gradual accumulation of metabolic products was a further factor which tended to reduce respiratory activity towards the end of the experiment.

It is difficult to assess the tolerance of adult *Palaemon* to the presence of ammonia in the water over long periods. In the first experiments larvae were utilized, because they were easier to handle in numbers, required very small volumes and were likely to be less tolerant than adults. Larvae were subjected to ammonia concentrations ranging from 0.2–200 mg/l, all of these being in excess of those found in normal sea water (less than 0.05 mg/l). The dilutions were standardized by the Nessler method after being prepared to approximate specifications from ammonia of 0.88 specific gravity. It was found that most solutions which were lethal (i.e. all those above 21.3 mg/l) took effect within an hour; the situation was little changed after 24 hours, by which time animals in solutions containing 10.6 mg/l of ammonia and below were still living. These results were checked using adult prawns in 6-hour experiments; these animals were found to succumb to a slightly lower ammonia concentration, i.e. 10 mg/l.

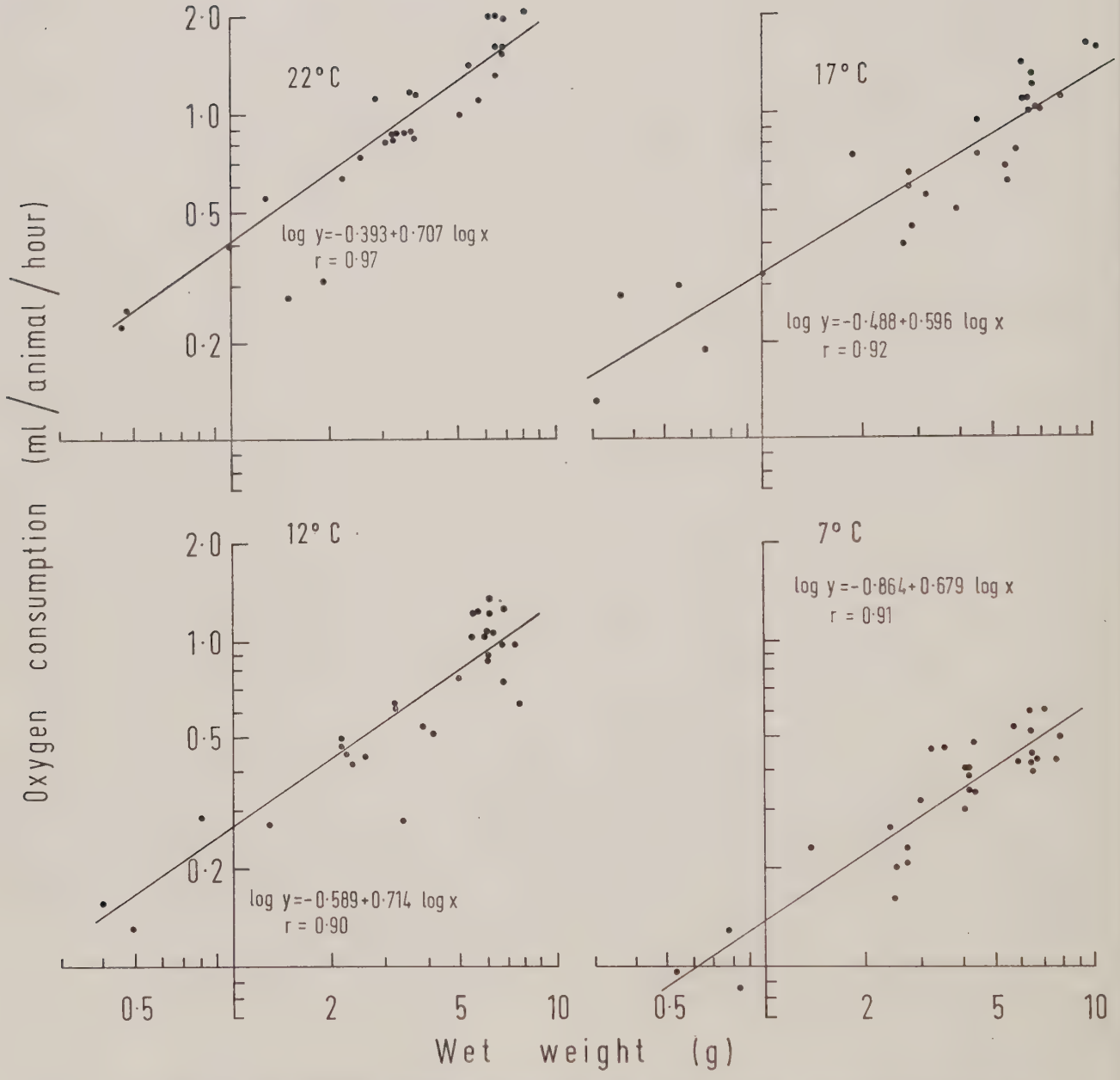


Figure 7 The relationship between oxygen consumption and wet weight in prawns maintained at temperatures of 22, 17, 12 and 7°C. The straight lines were fitted statistically.

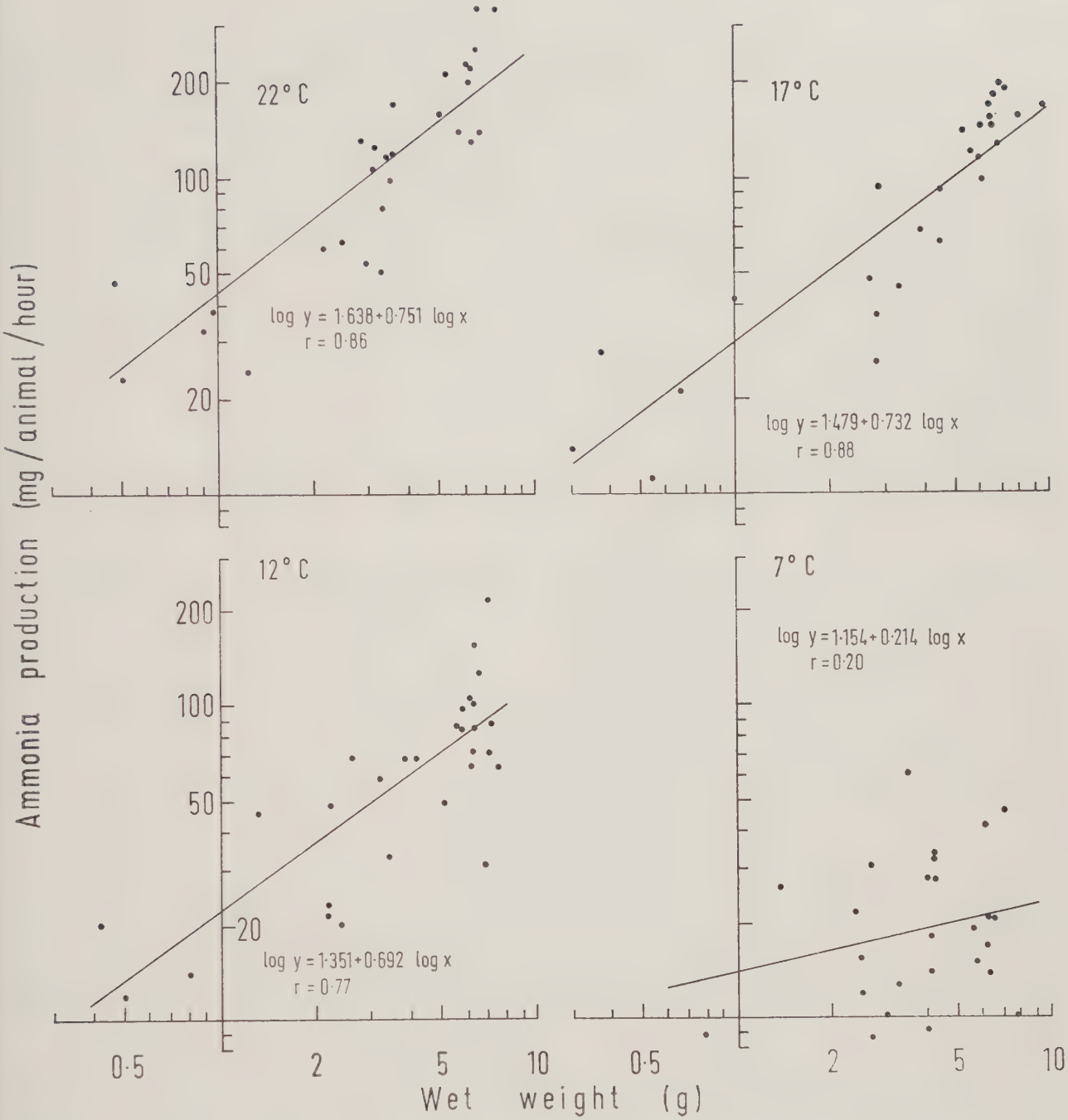


Figure 8 The relationship between ammonia production and wet weight in prawns maintained at temperatures of 22, 17, 12 and 7°C. The straight lines were fitted statistically.

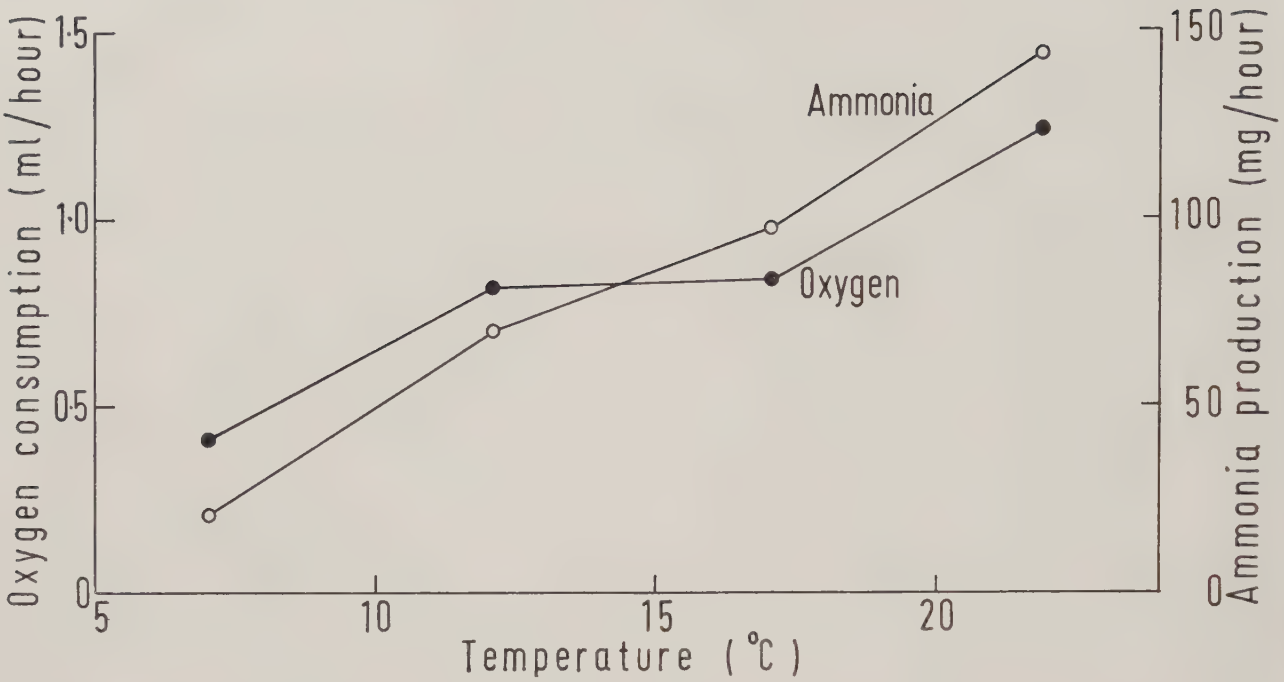


Figure 9 The oxygen consumption and ammonia production of a 5-g prawn at different temperatures.

DISCUSSION ON STOCK MAINTENANCE

It has been shown that in Britain dependence on the wild stocks of *P. serratus* for the provision of breeding populations is an inherently hazardous position, by virtue of the susceptibility of this species to unusually cold conditions. Although the cockle, which was similarly affected in the winter of 1962/63, made a very rapid recovery in many areas when conditions favoured a good spat-fall, prawn stocks are only gradually recovering over a period of several years. This phenomenon is doubtless related to the prawn's fecundity, which is measured in hundreds rather than in millions. Hudinaga and Miyamura (1962), in discussing the rearing of shrimps commercially in Japan, remarked on the necessity of ceasing to rely on natural populations for breeding stock, although at that time spawning in captivity had not been achieved. Hughes and Matthiessen (1962) reported that lobsters mated and spawned in the Oak Bluffs Hatchery, but never held their eggs long enough for them to hatch. Successful spawning, i.e. that which led to viable larvae which could be reared through metamorphosis, occurred quite frequently in mixed populations of *Palaemon serratus* brought into the Conway laboratory. No experiments have yet been made to investigate optimum conditions, nor has any information been gathered on the rate of maturation of the gonads in the laboratory. It was noticed on some occasions that the eggs were very few in number, or that they were sometimes lost during the period of egg carriage. It is not known whether this occurs in nature, or whether faulty copulation was induced by laboratory conditions. According to Jefferies (1964) detailed observations on *Palaemonetes varians* showed that females which lost eggs either did so within the first hour, or (more commonly) within the first week. The latter event, he stated, was due to deficiencies in the 'cement' binding the eggs. Höglund (1943) found that eggs of *Palaemon elegans* which were not fertilized were lost immediately.

In females already berried when taken from the sea, the greatest hazard affecting the realization of the maximum number of larvae to be obtained from the mother was the latter's cannibalistic tendencies, which are doubtless responsible for the scatter of points in Figure 3. For this reason, in large-scale routine hatching, larvae were separated from their parents as soon as possible by attracting them to the tank outflow where they were swept into another container. There were always a few eggs remaining around the abdominal ventral region of the mother after hatching, but these were so few as to be easily counted by eye. It was unusual to find more than 30 dead larvae out of 2 000 within the first day after hatching. Consequently it is difficult to account for the discrepancy between the number of eggs carried, as determined by Forster (1951a) and myself (Figure 3), and the maximum numbers of viable larvae hatched out. The difference was more pronounced in smaller prawns. It is possible that not all the dried particles counted from a berried animal were developing eggs destined to become larvae.

It is not clear why commercial potters and trawlers are currently (1966) restricting their fishing to a period between October and March. The observations of Forster (1951a) on seasonal movements indicated that prawns move offshore in winter and onshore in summer. It is possible that the areas commercially fished, which were well below the level of low tide (in a particular case by about 20–30 ft), would be considered offshore as far as this species is concerned. Before the hard winter of 1963, however, fishery statistics indicate that there were substantial catches during the summer months. The author gained the impression that the men were now finding that lobster fishing was more lucrative during the summer, and so were not expending too much effort in searching for prawns.

From the information to hand, it can be predicted that the annual period during which larvae are obtainable in the laboratory can be extended well beyond that during which they occur in the sea. By hatching out eggs from females which had spawned in the laboratory but were already mature when taken from the sea, the first larvae of the season were obtained on 7 December 1965. From the work of Forster (1951a) it can be seen that in the Plymouth region the first larvae do not appear in the sea until the following March; in North Wales their appearance would be even later (Cole 1958). Those prawns which hatched their eggs earliest in the Plymouth region would then spawn a second time, and berried females could then be found until July. At Holyhead (North Wales), I have taken a few berried females at the beginning of August, although all these were approaching full-term. From the foregoing remarks it can be seen that by increasing the experimental temperature and accelerating the onset of spawning and egg development in the autumn, and by lowering the temperature and retarding the process in animals taken in the late

spring and early summer, it should be possible to obtain a supply of larvae from December to the following September. This projected 10-month period of larval availability assumes that mature and berried females will be obtainable from the natural environment as required.

The act of moulting appears to take place in a manner similar to that described for *Palaemonetes* by Jefferies (1964) and for *Palaemon elegans* by Höglund (1943), the exuvium usually remaining in one piece. Prawns which were confined individually showed no overall tendency to grow, although they moulted regularly. The fact that some prawns would consistently lose or fail to gain weight on moulting seems to indicate that the moulting cycle is rigidly fixed, and that it is geared largely to time and temperature. Although it may be true, as is often stated (e.g. Passano 1960), that moulting is the only method by which an animal with an exoskeleton can grow, it cannot have been the pressures of growth which caused moulting in this case. Growth might have occurred if the prawns had been maintained in conditions less unnatural than these (isolated in beakers), although similar results have been obtained with tank populations. It is possible that these animals, many of which were near to the maximum size for their sex, as determined by the largest size of prawns taken from the sea, would not grow much further in any case, However, if this were so, they might also be expected to cease moulting (Passano 1960). Fielder (1964), discussing growth in captive decapods, noted that only rarely was moulting in *Jasus* not accompanied by growth, but Travis (1954) found both a lack of weight increase and also a weight decrease on moulting in *Panulirus*.

In the few adults which did show some weight increase a pattern similar to that shown by Travis (1954) for *Panulirus* and by Kurata (1962) for various species was observed. At the moult there was a large loss of weight, due to the loss of the old exoskeleton, followed by a weight increase which continued throughout the intermoult period. In animals which showed very little change in weight through successive moults, the weight loss at ecdysis must presumably have been approximately equalled by the weight gain during the intermoult period (i.e. 4.5–6.5 per cent of the total weight).

Although the cannibalism of soft newly-moulted prawns is not a phenomenon confined solely to non-natural conditions (Jefferies 1964), it is inevitable that such tendencies must be aggravated in tank populations. Apart from the overcrowding of animals far beyond conditions to be found in the sea, the small size of the tanks (3 ft $\times 2\frac{1}{2}$ ft $\times 1$ ft) restricted the attempts of soft prawns to escape attack. Even with the addition to a tank of all kinds of objects in which a soft prawn could take partial refuge, it was not long before one or more of his fellows found him; it was then a question of whether he could hold off the would-be cannibals until his exoskeleton had hardened. As would be expected, there was an inverse relationship between the density of animals in a tank and the chances of a soft prawn remaining alive during this critical period (Figure 5).

The mortality of soft prawns, and the deaths caused by 'brown spot' and 'white spot' symptoms were important factors in the decline of populations of laboratory stocks. Mortality attributable to the latter effects occurred sporadically throughout the year, and further work might indicate definite correlations with the seasons, though animals maintained below 10°C did not seem less susceptible to infection. It is interesting to note that these appearances of infection have not so far been found in prawns which have been reared in the laboratory from the egg, despite the fact that one population reached a mean length of over 5 cm in 190 days. As this population was contemporary with adults from outside which were showing the symptoms, it is likely that the laboratory sea water supply, common to all, was not suspect. The outside prawns may have brought with them a microbial flora, normally non-pathogenic in nature, which in the unnaturally crowded conditions of the laboratory tanks, where the prawns may have been under considerable stress, became pathogenic. In these conditions, the bacterial count of the sea water was found to have increased several-fold, even under conditions of water circulation. The chitinoclastic bacteria which were found to be responsible for 'shell disease' (Hess 1937) have since been found in sea water, on crustacean exoskeletons and in their guts (see Seki and Taga 1963).

Another major cause of mortality in stock prawns may have been the inadequacy of the diet. Evidence is weak on this point, consisting of the observation that apparently-healthy animals died just before moulting, and that this number increased with time in captivity.

Oxygen consumption was measured for *Palaemon serratus* by Scheer and Scheer (1954) although no experimental temperatures were given, which makes comparison of little value. Cohnheim (1912) reported values of between 99 and 131 μl 0_2/h/g (wet weight) at temperatures between 13 and 17°C, which correspond

well with the curve in Figure 7. From this figure it can also be seen that the relative rate of oxygen consumption varied inversely with the size of the prawn; the oxygen consumption (per gramme) of a 1-g animal is about twice that of a 10-g animal. The actual values for the slope lie between 0.6 and 0.7. A similar figure was obtained by Teal (1959) for the crab *Uca pugnax*, although an average result for 54 crustaceans was given by Zeuthen (1953) as 0.83.

The rate of change of oxygen consumption with temperature varied, and over the size range from 2 to 10 g wet weight there was no significant increase between 12 and 17°C. Taking the experimental temperature range as a whole (7–22°C) the overall Q_{10} for oxygen uptake was 2.1; this value was independent of the weight of the animal, and it is rather lower than that for many other crustaceans, in which it ranges between 2.0 and 3.0 (Wolvekamp and Waterman 1960). Between temperatures of 7 and 12°C, 12 and 17°C, and 17 and 22°C the Q_{10}s were 4.2, 1.2 and 1.9 respectively. The Q_{10} value increased more rapidly at low than at high temperatures, a phenomenon common to other crustaceans (Wolvekamp and Waterman 1960).

Adult prawns appeared to be independent of the external concentration of oxygen over a range from saturation down to about 50 per cent saturation (Figure 10). Below this, the respiratory rate decreased sharply, and at an external oxygen concentration of 0.5 ml/l (about 8 per cent saturation) the animal ceased to take up further oxygen and died. Although the curve is hyperbolic, the point at which regulation begins to fail (sometimes called the critical concentration or tension) is fairly sharply defined. Similar regulatory abilities occur in *Uca* (Teal 1959), but not in *Homarus* (Thomas 1954).

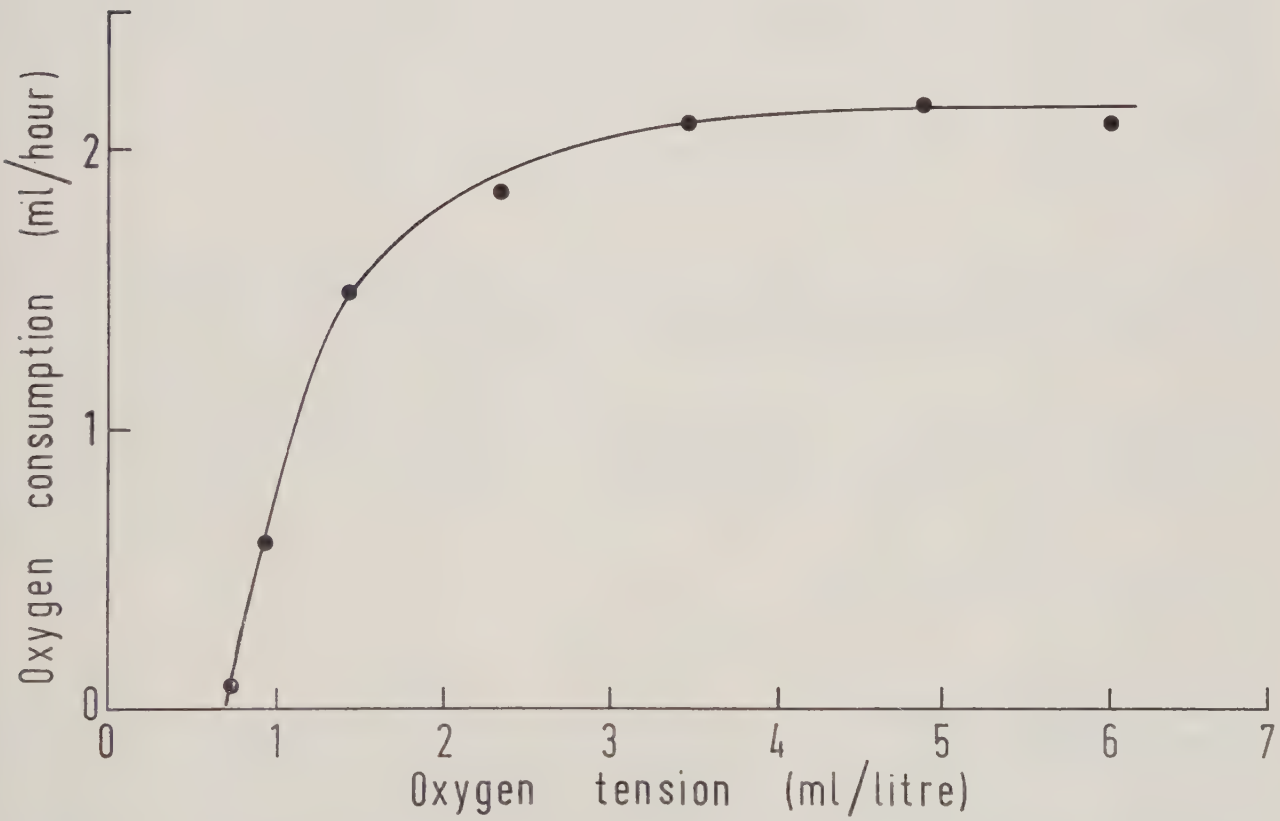


Figure 10 The relationship between the oxygen consumption of a 5-g prawn and the oxygen tension of the medium.

Using the above data, tank volumes for prawn populations which will allow short-term storage in still water can be estimated. The degree of water circulation and re-oxygenation necessary in long-term storage tanks may also be derived. In Table 1*a* the number of hours required for 100 prawns to reduce the oxygen in 100 litres of saturated sea water to 50 per cent saturation has been calculated, for animals of 1 and 10 g wet weights. Saturation values have been taken from Table 20 of Barnes (1959). Such calculations can only be approximate, since they assume the water to be efficiently mixed, but take no account of atmospheric diffusion of oxygen into the water. Table 1*b* tabulates the number of litres per hour of saturated water required to replace the oxygen taken up by the animals under the conditions already mentioned; these figures could be used as an indication of the required hourly flow rate of water through the tank as a percentage of the total volume. This rate will be underestimated, since it is impossible in practice to ensure instantaneous mixing.

The excretion rate of ammonia in *Palaemon* was chosen as a suitable subject for the investigation of nitrogenous excretory products because ammonia is known to comprise the greater part of the total nitrogen output in Crustacea, and also to be the most toxic component (Parry 1960). The great scatter of points at 7 °C and the correspondingly low correlation coefficient (Figure 8D) are largely reflections of the fact that the amounts of ammonia produced at this temperature were so small that the analytical method was being used at the limits of its sensitivity.

Although the blood of mammals contains no more than 0.03 mg/l ammonia, that of the crustaceans *Homarus* and *Maja* contains up to 18 and 24 mg/l respectively (see review in Prosser and Brown 1961). It is therefore not surprising to find that *Palaemon* larvae can survive for over 24 hours in dilute solutions of ammonia (concentrations of up to 20 mg/l). This information has been used to calculate the data of Table 1*c*, which shows, for the same conditions as in Table 1*a*, the time elapsing before a lethal concentration of ammonia builds up. It can be seen that a period some sixty times longer than that at which oxygen concentration would be reduced to 50 per cent saturation (critical concentration) would be required before a lethal level of ammonia would be reached. This assumes that ammonia is not being lost to the atmosphere, or being liberated by decomposing food, and that the tolerance of adults is similar to that of larvae. In tank populations, therefore, conditions which allow sufficiently high oxygen concentrations to be maintained in a circulating system would almost invariably ensure a very low level of ammonia relative to the tolerance of the prawn. An exception to this might occur in the presence of large quantities of decomposing food.

Table 1 The effect of prawn size and water temperature upon the rate of depletion of oxygen and accumulation of ammonia, for 100 prawns in 100 litres of sea water

	Weight per prawn (g)	Temperature (°C)		
		22	12–17	7
a Time (hours) required to reduce oxygen-saturated sea water to 50 per cent saturation	1	6.25	9.70	25.2
	10	1.25	2.24	5.30
b Number of litres/hour of oxygen-saturated sea water required to replace the uptake of oxygen	1	8	5	2
	10	40	22	9
c Time (hours) before a lethal level of ammonia is reached	1	455	770	1 430
	10	82	143	834

SURVIVAL AND GROWTH OF YOUNG STAGES

GENERAL

The first section of this paper concerned the methods of obtaining and maintaining a stock of the prawn *Palaemon serratus* (Pennant), and also the acquisition of larvae from berried females in the laboratory. The following pages contain an account of the effect of various physical and biological factors on the rearing of the larvae thus obtained. In some cases only the larval life has been considered, but more often the experiments were extended over the metamorphosis period; in one case animals were reared well beyond metamorphosis and through their juvenile phase.

In the experiments to be described below, the standard method of rearing was to utilize larvae hatched during the previous night. These were washed in several changes of sea water which had been twice filtered (first through sand and then through ceramic candles) and irradiated by ultra-violet light (Walne 1966). One-litre beakers and sometimes polythene buckets were used as experimental vessels; they were provided with small-bore glass tubes for aeration purposes, and stood in water baths at 20–22 °C. The salinity of the water was 31.5–32.5‰, except for rare periods when it fell somewhat below this figure. Standard food was provided in the form of nauplii of *Artemia salina* which were hatched out in ordinary sea water, as required, from commercial dried eggs. The unfed *Artemia* nauplii were normally utilized within 24 hours of hatching. They were separated from their egg cases, either by swirling the water to collect the nauplii at the centre of the bottom of the vessel, or by making use of their attraction to light. Three or more times each week the water and food in the prawn cultures were completely renewed. Except where specifically detailed, these conditions were maintained in all the following experiments.

TREATED AND UNTREATED WATER

Oyster larvae have been routinely reared in filtered and irradiated water for several years at this laboratory. They were shown to respond unpredictably to untreated water (Walne 1966), and the treated water usually (though not invariably) produced the best growth and survival. For this reason, and also because treated water closely approached a standard medium, by virtue of the absence of fluctuating amounts of particles above 5 μ in size, it was used in the prawn work.

When prawn larvae were reared in both treated and untreated water in four experiments there was a variable increase in mortality in those populations in the untreated water (Table 2). Duplicate experiments were carried out at various larval densities and for various lengths of time, in polythene buckets. The overall mean difference in the percentage survival between larvae in treated and untreated water was 5.3 per cent per week.

DARKNESS

Prawn larvae are strongly positively phototropic and tend to concentrate themselves in a very small percentage of the total volume of any vessel in all but the most rigorously uniform of lighting conditions. It is not uncommon to find that over 95 per cent of 10 000 larvae known to be in a 200-litre tank have gathered at one corner, occupying 2–6 litres of the available space. Such concentrations might tend to produce local shortages of food and oxygen in their vicinity, and would certainly increase tendencies towards cannibalism. Animals kept in total darkness would not tend to concentrate themselves artificially in this manner, and hence survival might thereby be increased.

Experiments were therefore set up, in a manner similar to those detailed in the previous section, in which the survival of prawns reared in darkness was compared with that of those reared under natural lighting conditions. In every case, the animals kept in darkness survived less well (Table 3), the overall mean weekly difference in percentage survival being 12 per cent. The dark-adapted prawns were almost colourless compared with the richly pigmented control animals.

Table 2 The difference between survival of prawn larvae in treated and in untreated water in four experiments

Experiment	Duration (days)	Initial number of animals	Final survival %		% difference in survival per day
			In treated sea water	In untreated sea water	
A	19	460	24	10	0.74
B	15	200	66	47	1.27
C	13	200	61	58	0.23
D	23	900	17	16	0.09

Table 3 The difference between survival of prawn larvae in daylight conditions and in darkness in four experiments

Experiment	Duration (days)	Initial number of animals	Final survival %		% difference in survival per day
			In the light	In the dark	
A	9	555	51	42	1.0
B	22	200	40	27	0.59
C	9	240	62	19	4.8
D	23	900	17	7	0.44

AGITATION

The provision of some form of agitation in vessels containing any but the lowest density of larvae is essential in order to facilitate gaseous exchange; the degree of agitation, in the form of air bubbled through the medium, need not be very great to achieve this. Also, by increasing the aeration, and consequently the degree of stirring of the water, the larvae will tend to be more evenly distributed and hence should have less opportunity for chance encounters leading to cannibalism.

In order to test this, 50 larvae were placed in each of six pairs of beakers. In the first pair, no aeration was provided; in the others, aeration was provided through a glass tube of internal diameter 6 mm, which extended to the bottom of the beaker. The five progressive degrees of aeration were:

1. no aeration;
2. 1–2 bubbles/sec;
3. 4–5 bubbles/sec;
4. continuous single stream of bubbles, little surface turbulence;
5. continuous double stream of bubbles, considerable surface turbulence;
6. continuous multiple stream of bubbles, violent surface turbulence.

The experiment was continued for 8 days. The final mean lengths and percentage survival of the prawn larvae are recorded in Figure 11, which shows that although there was little difference in survival and growth at the lower end of the agitation scale, at the upper end both were adversely affected. Mild agitation conferred no benefits in increased survival when animals were not present in a density high enough to deplete the oxygen tension markedly; on the contrary, even moderate agitation tended to reduce both growth and survival rate. Similar results were obtained in an experiment in which bubble size was varied (with a range of air-tube diameters), rather than bubble frequency. Similar experiments have also been performed using air-diffusers in 25-litre bins; vigorous aeration, even with the very small bubbles, again produced very high mortalities.

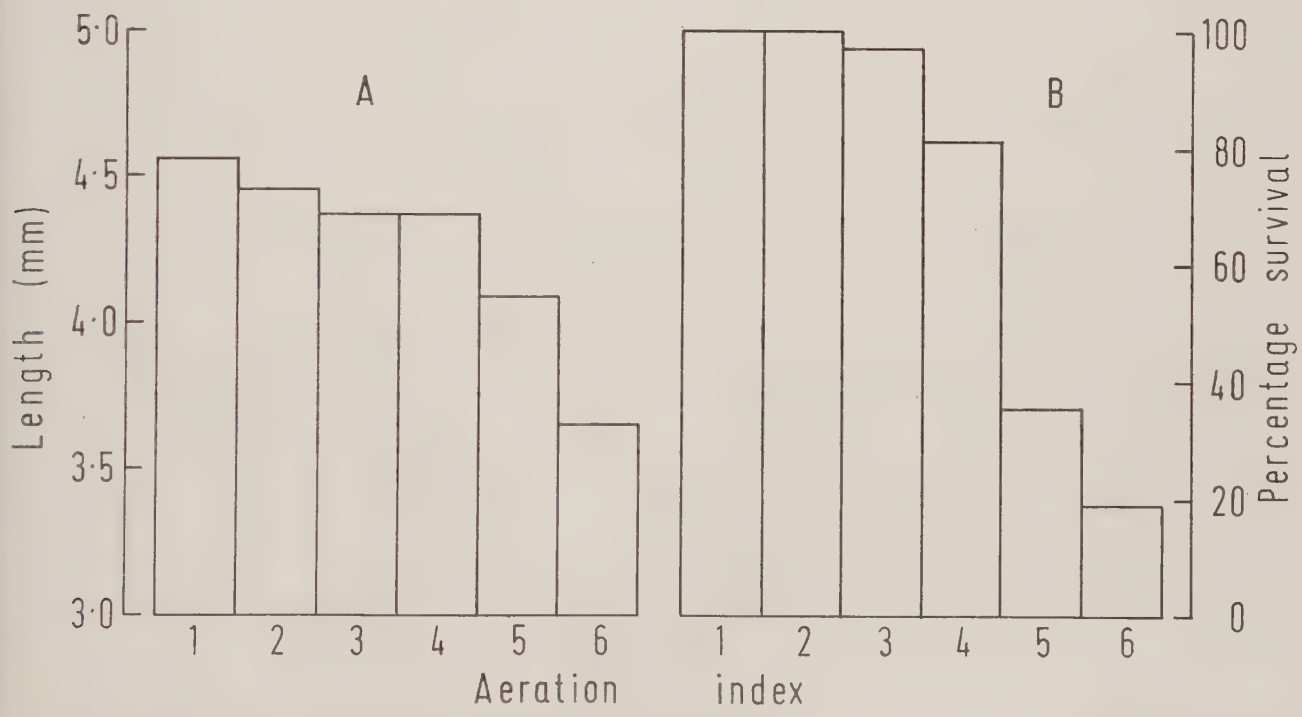
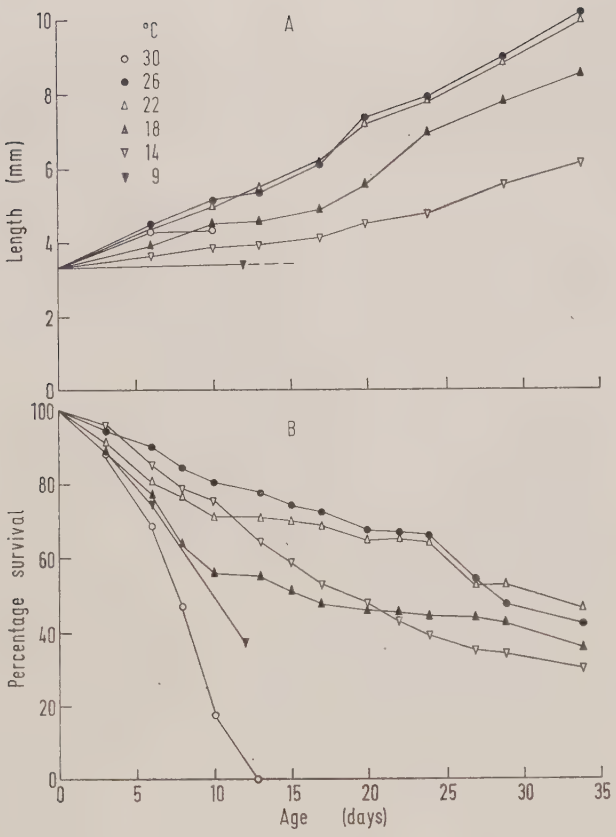
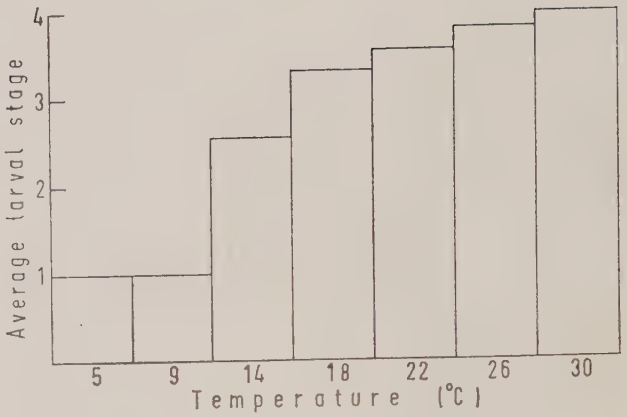


Figure 11 The effect of increasing agitation (bubbling) on (A) growth and (B) survival of larval prawn populations. For the aeration index, see text, above.





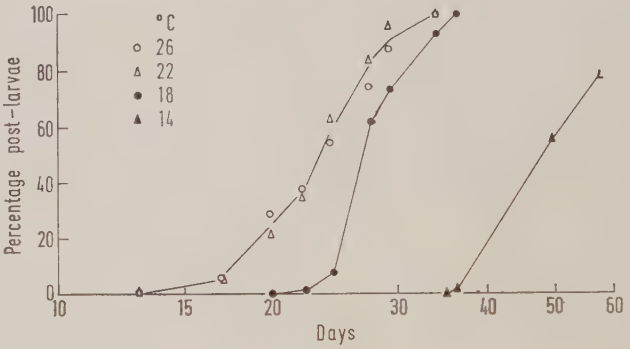
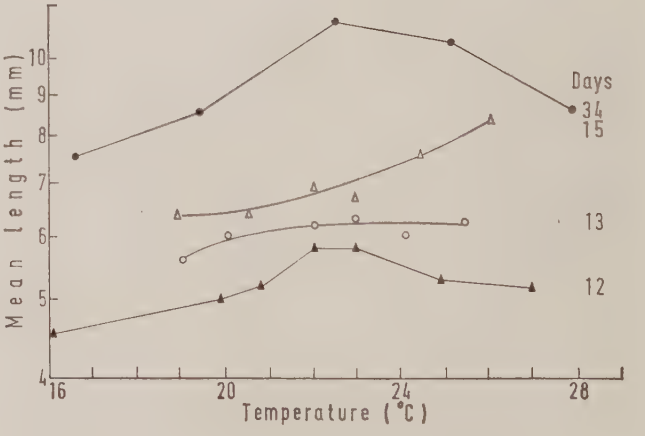


Figure 12 Above The effect of six different temperatures on (A) growth and (B) survival of larval prawn populations.

Figure 13 Top right The average larval stage reached after six days by larval prawn populations at seven different temperatures.

Figure 14 Centre right The relationship between metamorphosis and age in days (log scale) for larval prawn populations at four different temperatures.

Figure 15 Right The effect of temperature on the growth rate of four single-brood larval prawn populations over various periods of time.



TEMPERATURE

The relationships between temperature, growth-rate and survival were studied over a temperature range from 5 to 30°C. The results of the most comprehensive experiment are summarized in Figure 12, which records the growth rate and percentage survival with age, at six temperatures. Duplicate experiments were carried out in polythene buckets containing 120 prawn larvae in 5 litres. At 30°C mortality was very high, no animals living beyond the thirteenth day. At 26 and 22°C, growth rate and survival after 36 days were very closely similar and were the highest of all the experiments; at these temperatures the larvae increased in length from 3.5-10 mm, with a survival of over 50 per cent. At 18 and 14°C, growth was progressively slower (8.5 and 6.0 mm final length respectively) and survival lower (35 and 30 per cent respectively). The larvae kept at 9 and 5°C showed no measurable growth after 12 days, although four of those at 9°C had moulted through to the second larval stage. Experiments at these two temperatures were then discontinued, and the results for 5°C are omitted from Figure 12.

After the first 6 days, the intermoult stages reached by samples of larvae from these experiments were determined microscopically, and mean values are shown in the histograms of Figure 13. At this age (6 days from hatching) there was a positive correlation between larval stage and temperature throughout the experimental range.

Figure 14 contains information on the progress of metamorphosis at 26, 22, 18 and 14°C. Again the larvae that were kept at the first two of these temperatures exhibited similar characteristics; the first post-larvae appeared on day 17, and metamorphosis was completed by day 34. At 18°C, although the process did not get under way until day 22, metamorphosis was completed more rapidly. The 14°C experiment was allowed to continue beyond day 36 up to day 49 in order that the course of its considerably delayed metamorphosis could be plotted. Taking as an index of the duration of larval life the age at which 50 per cent metamorphosis had occurred, the mean lengths at that age of the populations at 26, 22, 18 and 14°C were 9.2, 9.2, 9.0 and 9.1 mm respectively.

According to the curves of Figure 12, the optimum temperature for survival and growth lay between 22 and 26°C. In order to investigate more closely the growth rates at temperatures around these values, a further four series of experiments were simultaneously run in a similar manner to those described above. In this case, however, instead of obtaining larvae from a mixture of several broods, offspring from single broods only were employed in each series at densities of 50 per one-litre beaker. The experiments were continued for 12–34 days, and the final mean lengths of larvae at each temperature are plotted in Figure 15. The 12, 13 and 34 day series confirmed the result of the earlier experiment, which indicated a maximum growth rate at temperatures of between 22 and 26°C. There was a definite peak growth rate at about 22.5°C in the 12 and 34 day experiments, but the curve of the 13 day experiment is almost flat over the range 20–25°C. In the 15 day experiment, growth rate increased over the entire temperature range of 19–26°C.

This disparity in mean growth rates between different experiments with regard to temperature variations in the range 20–27°C appeared to be connected with the fact that the larvae originated from various broods. This variation in response between the offspring of different berried females was therefore investigated at one temperature (22°C). One series of eight replicate experiments was set up containing newly-hatched larvae, all from the same female, and a further eight containing larvae from eight different females. After 30 days the mean lengths of the former eight populations ranged from 7.56–8.12 mm, while that of the latter ranged from 7.83–10.80 mm. Further evidence of physiological differences between broods will be given below.

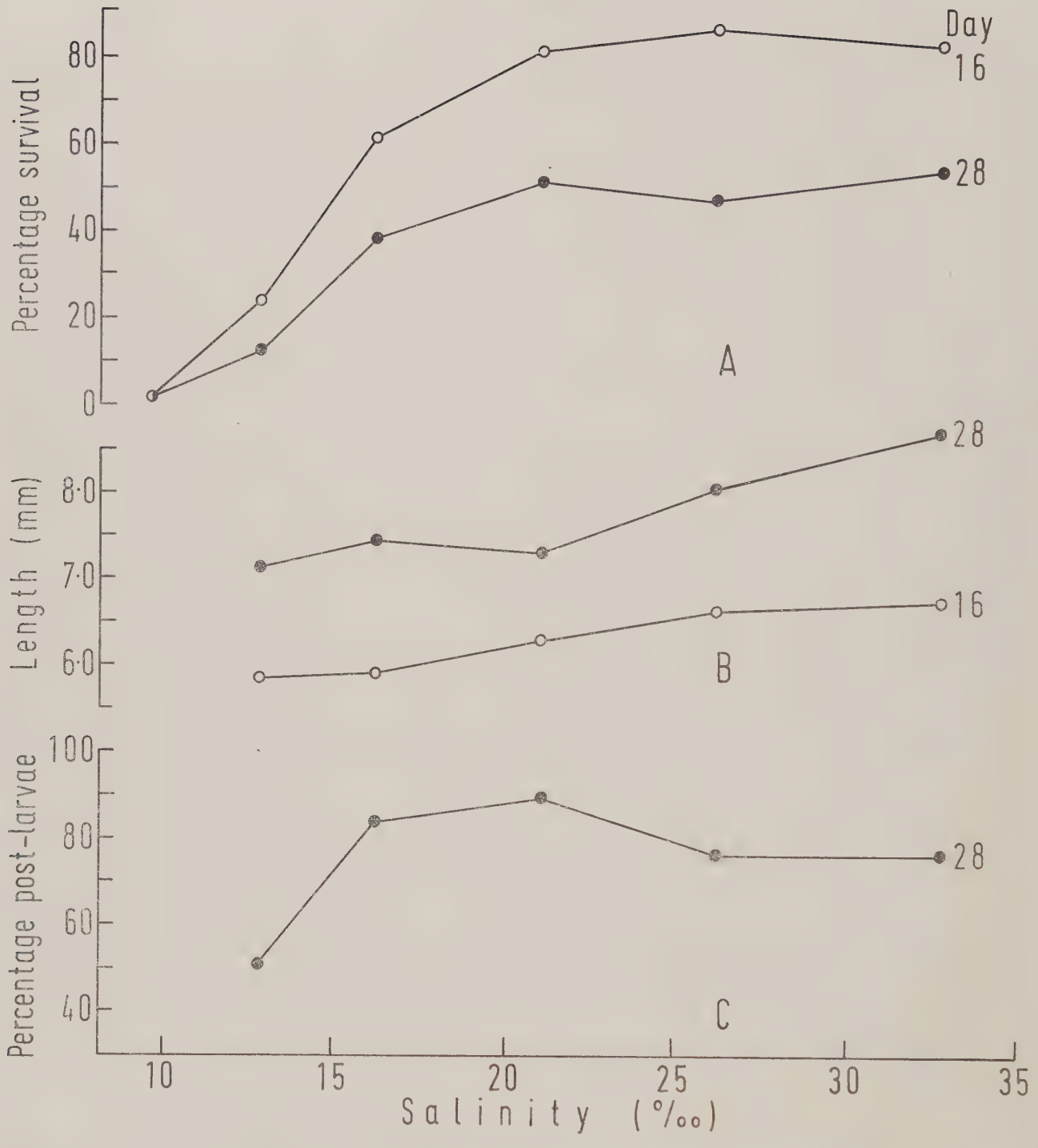


Figure 16 The results of experiments made to show the effect of salinities ranging from 10–32.5‰ on the survival, growth and metamorphosis of prawn larvae.

A. Percentage survival at days 16 and 28.
B. Average size at days 16 and 28.
C. Percentage of surviving animals which had metamorphosed by day 28.

SALINITY

Although drastic changes in the salinity of the laboratory sea water supply do not occur frequently, there are occasional abnormal weather and tidal conditions which necessitate water of lower salinity being used in order to maintain the laboratory circulation. The first salinity experiment was carried out to find the range of tolerance of 100 newly-hatched prawn larvae, which were transferred from water at 32.5 $^0/_{00}$ to salinities ranging from 6–55$^0/_{00}$. Transference was made in one step in order that effects of sudden rather than gradual changes could be assessed. Salinities lower than that of the local sea water were obtained with de-ionized water; higher salinities were produced by allowing partial evaporation to take place prior to experiments.

The percentage survival after 4 days was recorded. All the larvae died within 12 hours in salinities below 10$^0/_{00}$ and above 52$^0/_{00}$; there was a 50 per cent survival rate in salinities from 15–45$^0/_{00}$ and a 95 per cent survival rate in salinities from 26–39$^0/_{00}$.

Since values lower rather than higher than the salinity at Conway (32.5$^0/_{00}$) were more likely to occur, experiments extending over the whole larval life utilized salinities ranging from 30–100 per cent of the full Conway salinity (10–32.5$^0/_{00}$). Duplicate experiments at six salinities were set up in one-litre beakers, each containing 50 newly-hatched larvae. Animals to be reared in salinities below 23$^0/_{00}$ were acclimated gradually over the first 3 days by progressively reducing the salinity below that value; even so, all those held at 10$^0/_{00}$ had died in the first 4 days. This is in contrast to another similar experiment in which larvae at this salinity died gradually over a period of 20 days. The results, shown in Figure 16, have been expressed differently from those in the previous section on temperature effects, because the differences resulting from various salinity treatments were less marked and would have produced a rather confusing picture. Instead, percentage survival and length (Figures 16A and B respectively) have been drawn for two different ages (days 16 and 28) to illustrate the consistency of the results. It can be seen from Figure 16A that survival was little affected by salinities above 23$^0/_{00}$, but below this it was progressively reduced. On the other hand, Figure 16B suggests that growth rate and salinity were directly related over the whole range, although the slope of the curve is not very great. Figure 16C, in which is recorded percentage metamorphosis on day 28, suggests no relationship between metamorphosis and salinity, except perhaps a tendency to delayed metamorphosis at the lowest salinity.

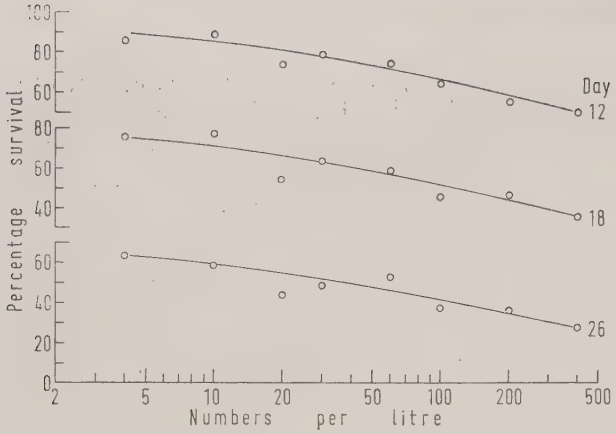


Figure 17 The percentage survival of populations of prawn larvae at initial densities ranging from 4 to 400/1 at three ages (days 12, 18 and 26).

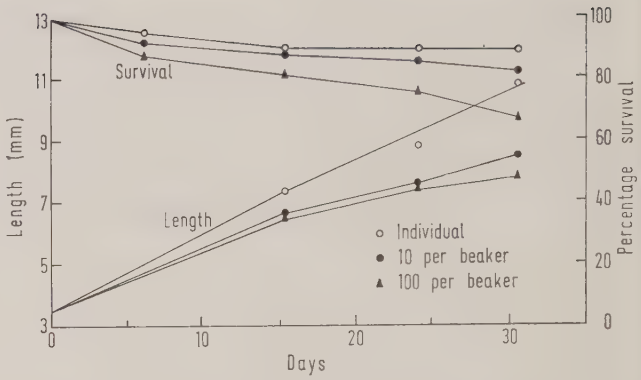


Figure 18 The growth and survival of three populations of prawn larvae at different densities, the lowest of which consisted of isolated animals in individual containers.

Table 4 The effect of cannibalism by post-larvae and late larvae on newly-hatched larvae, shown as the numbers of the latter remaining after three days

Initial numbers of newly-hatched larvae	Experiment 1 Initially 10 post-larvae		Experiment 2 Initially 10 late larvae		Experiment 3 Control
	Post-larvae	Newly-hatched	Late larvae	Newly-hatched	Newly-hatched
10	9	2	10	5	8
20	10	0	10	15	20
40	10	7	10	28	37
80	9	8	10	49	69

DENSITY AND CANNIBALISM

In the first of these experiments, eight duplicate larval series were set up in buckets containing 5 litres of sea water, using larvae from a mixed population of 10 000 which had hatched within 48 hours of each other from various berried females. Densities ranged from 20–2 000 larvae per bucket, or 4–400/1. Figure 17 plots survival at these densities on the 12th, 18th and 26th days after hatching, by which time the animals were almost at the end of their larval life. Survival at the end of the experiment (26 days) ranged between 28 per cent at the highest and 64 per cent at the lowest density.

It is difficult to determine with certainty the main factors which led to a higher proportion of deaths at higher densities. Food was maintained in excess and the water was constantly aerated. Bacterial build-up and accumulation of metabolic products would inevitably be greater at the higher densities, and to reduce these effects the water was changed and the buckets cleaned three times each week. Living larvae were often seen to be grasping hold of each other, presumably in an attempt at cannibalism, although there was no way of deciding whether one of these was about to die from other causes. Dead animals were also seen to be grasped in this way, and such animals were rarely found intact at the bottom of an experimental vessel at the conclusion of an experiment. It was clear at least that healthy larvae scavenged on dying or dead ones.

It could, however, be ascertained from indirect evidence that larvae consume each other in an actively cannibalistic fashion. The life-expectancy of isolated unfed newly-hatched larvae was found to be of the order of 5 days. However, out of a population of 100 in a one-litre beaker only 50 per cent survived by the 6th day and 10 per cent on the 11th day, although very few corpses were found. Clearly, the stronger, or perhaps the faster growing, larvae survived longer at the expense of the others.

Cannibalism might also be inferred if the death rate in a population of animals was higher when a small proportion of larger animals was introduced, other factors being the same. Three experiments were therefore set up, each comprising four replicate beakers containing newly-hatched larvae at densities of 10, 20, 40 and 80 per beaker; in the first experiment 10 post-larvae of length 11 mm were put with the newly-hatched larvae, and in the second 10 late larvae of length 7.5 mm. The third experiment (the control) contained only the newly-hatched larvae. The surviving animals were counted after three days, and the results are shown in Table 4. All except two of the post-larvae and all the late larvae survived. The early larvae in experiments 1 and 2 showed, however, only 12 per cent and 66 per cent mean survival respectively, compared with 90 per cent survival in the control. No dead larvae were found.

In the experiments so far described it has been impossible to estimate how much of the theoretical 100 per cent maximum survival rate might be achieved, over the whole of the larval life, under the best rearing conditions obtainable in the laboratory. In order to achieve what might approximate to optimum conditions for survival, 20 newly-hatched larvae were placed individually in separate one-litre beakers, and, for comparison, 10 larvae were placed in each of five beakers and 100 in each of three; all were from the same brood, they were all fed daily, and the water was changed daily. The results are summarized in Figure 18. The individual larvae produced the highest growth rate and survival and earliest metamorphosis; for these larvae a survival rate as high as 90 per cent was recorded after 31 days, which was 8 days after all had metamorphosed. Even the populations of 100 showed a 67 per cent survival rate, although growth of these and of the populations of 10 was slower than that of the isolated animals. In the populations of 10, metamorphosis was not complete until day 31, and in the populations of 100 until day 33; it was possible that food was more limiting in these populations, although efforts were made to ensure high food density. It was also possible that larvae were inhibiting each other's growth by slight accumulation of metabolic products in the water or by disturbance.

Table 5 The percentage survival, after fourteen days, of larval prawn populations under twelve different feeding regimes

Food	% survival
1. *Artemia* nauplii	43
2. Chopped ox liver	22
3. Chopped fresh mussel	20
4. Commercial fish food flakes, Brand A	17
5. Commercial fish food flakes, Brand B	15
6. None (control)	12
7. Dried Daphnia (sold as fish food)	10
8. 'Biol', described as dried plankton	10
9. Detritus, filtered from the local sea water	8
10. Dried ant eggs (sold as fish food)	7
11. Chopped seaweed	7
12. Dried *Chlorella*, suspended in the water in coarse lumps, because prawn larvae cannot ingest particles as small as single algal cells	5

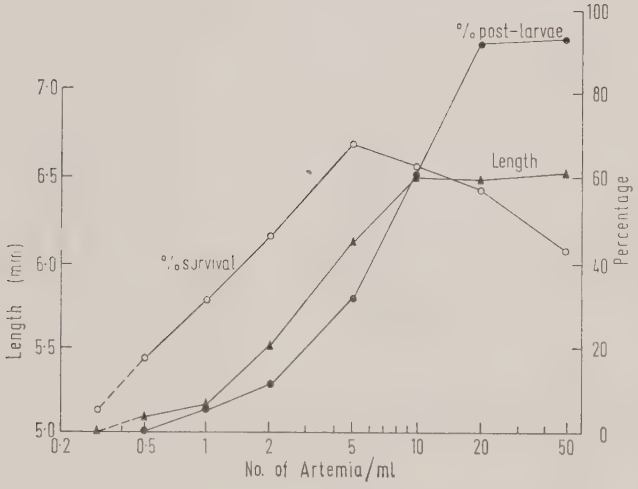


Figure 19 The relationship between food concentration and percentage survival, final size, and percentage metamorphosis for populations of prawn larvae. The points connected by a broken line refer to animals which were starved.

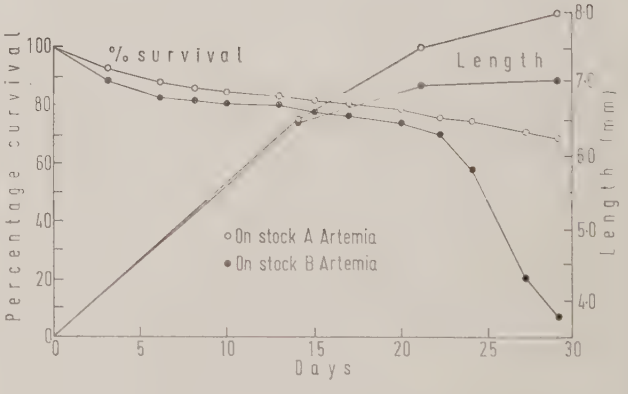


Figure 20 Growth and survival in two populations of prawn larvae, one of which was fed on stock A *Artemia* and the other on stock B *Artemia*.

FOOD

In preliminary experiments to test whether prawn larvae could feed on algal suspensions, *Isochrysis*, *Micromonas* and *Phaeodactylum*, in concentrations sufficient to faintly colour the sea water, were provided. In each case, the larvae survived no better in such media than in filtered sea water only.

The cannibalistic tendencies of the larvae, and their apparent ability to browse on mussel tissue, indicated that they were able to consume particles at least as large as themselves, and perhaps larger. A wide range of possible foods was consequently offered to newly-hatched larvae in populations of 50, and the percentage survival over 2 weeks in these experiments is presented in Table 5. There is probably no significant difference between the survival of the control animals and the slightly lower values for treatments 7–12, although the possibility of a poisoning effect cannot be excluded. Microscopic examination of the larvae indicated that they had certainly consumed quantities of *Chlorella*, detritus and dried plankton. Of treatments 1–5, which all yielded better survival than the control, the least successful, 4 and 5, used different brands of commercial fish food flakes. Better survival was obtained with treatments 2 (chopped ox liver) and 3 (chopped fresh mussel). Treatment 1, the live nauplii of *Artemia*, the brine shrimp, gave survival rates over twice as high as the next best. It is possible that the chopped liver and mussel are basically satisfactory foods, but in sea water at 20°C they very quickly deteriorate in quality, under the influence of bacterial activity, and cloud the water.

Similar comparisons were made between the usefulness of *Artemia* and mussel as food, using late larvae; these were over ten times larger (on a weight basis) than newly-hatched animals. It was considered possible that *Artemia* nauplii, which were about 0.5 mm in length, might be too small for the larger larvae; the results obtained, however, showed that survival was much higher with the live food. In three experiments lasting for one week, the mean survival rate of *Artemia*-fed animals was 45 per cent better than those fed on mussel. Larvae fed on mixtures of the two foods survived nearly as well as those fed on *Artemia* only. The survival of early post-larvae followed the same pattern, but in tests with older post-larvae (over 14.5 mm in length) the position was reversed, although the superiority of mussel was only very gradually apparent. In this experiment the mussel was not chopped, but left on the shell. Over 40 days, the mussel-fed population increased in length from 14.5 to 24.5 mm and achieved a 62 per cent survival rate, whereas the *Artemia*-fed animals reached a mean length of 19.0 mm with a 22 per cent survival rate.

It seemed that the prawns above 14.5 mm in length may have found it increasingly difficult to catch enough tiny (0.5 mm long) *Artemia* to satisfy their needs, and this raised the possibility of using *Artemia* which had themselves been reared to a larger size. One experiment was attempted in which 50 newly-hatched prawn larvae and 5 000 *Artemia* nauplii were placed in a bin through which was circulated water (from a supply normally used for oysters) which was enriched with algae; no further food was added. After 25 days, metamorphosis of the prawn larvae was complete, and 70 per cent of the animals remained. The mean length of the few remaining *Artemia* had increased from 0.5 to 2.0 mm.

From the above experiments, it was clear that *Artemia* provided the best available source of food for the larvae. Experiments were consequently undertaken to investigate the relationship between food concentration and larval growth and survival. Duplicate experiments were set up in one-litre beakers in which were placed 100 newly-hatched larvae of mixed parentage, together with sufficient *Artemia* to achieve initial concentrations of 0.5, 1.0, 2.0, 5.0, 10, 20 and 50 *Artemia*/ml. Both the sea water and the food in these series were completely changed every day. No attempt was made to maintain the initial food concentration throughout the 24-hour period, and consequently, although at the highest concentrations it was but little reduced, at the lower end of the scale most of the food was consumed within 24 hours. A control experiment to which no food was added was also included. The results are summarized in Figure 19; the curves for the mean percentage survival and the final length show the values obtained after 16 days, by which time very few of the control (starved) animals remained.

The highest survival rates were obtained in populations at initial feeding concentrations of 5–10 *Artemia*/ml; at the highest food concentration survival was markedly lower. Larval growth and food concentration were directly related up to a feeding level of 10 *Artemia*/ml, above which no further advantage in growth rate was achieved. On the basis of the growth and survival rate curves it would appear that a food density of about 10/ml would be about the optimum feeding level under these experimental conditions.

Figure 19 also shows the percentage of larvae which had metamorphosed by the 26th day. The overall relationship between high food concentrations and early metamorphosis again occurs, but in this case the levelling off at the highest food concentrations is less marked. This discrepancy may be due to the fact that the population was 10 days older by this time, and the larger animals would be needing more food and perhaps benefiting from the highest concentrations.

During the course of this study the source of supply of the brine shrimp eggs was changed, and it became obvious that two different types of *Artemia* were being supplied. It is difficult to trace their origins, since both were obtained through agents rather than directly from the producer, but it is known that the original stock A came from California, whereas stock B came from Utah. They were easily identified, because the eggs of stock A tended to float in sea water and those of stock B sank; there were also slight differences between the two stocks in the percentage of viable eggs and in the sizes of the emergent nauplii. Some time after this change in the source of supply of *Artemia*, several larval prawn populations failed to metamorphose successfully. For this reason a correlation was sought between *Artemia* eggs from different sources and larval metamorphosis. Larvae from each of ten different broods were divided into duplicate experiments, which were fed with *Artemia* from sources A and B respectively. In Figure 20 are shown the results for a typical pair from the same brood; all the pairs showed similar characteristics. For most of the larval life there was little difference in the growth rate and survival of larvae fed on the two stocks of *Artemia*. At metamorphosis, however, the larvae fed on stock A moulted into normal post-larvae, whereas those fed on stock B appeared to be unable to complete the moult, by failing to rid themselves completely of the exuvium, especially from around the pereiopods. They showed much less activity and tended to spend most of their time lying, often on their side, on the bottom of the vessel; their antennae were kinked in several places instead of being shaped in the usual graceful curve, and within 1 to 5 days they invariably died. The post-larvae fed on *Artemia* stock A continued to moult and grow normally (Figure 20). Similar differences have been observed in fish larvae fed with *Artemia* from the two sources (M.A.F.F. 1967).

In an experiment in which similar pairs of larval series were all fed on stock B for the first 10 days, those which were subsequently transferred to stock A food metamorphosed successfully.

A further experiment, using larvae from the same brood, was set up to discover the effects of mixing the food stocks. The series was made up of six populations, each of 100 larvae, in which the proportions of stock A to stock B *Artemia* in the food were (in percentages) 0:100, 5:95, 10:90, 20:80, 50:50 and 100:0; the results are presented in Table 6. In the populations offered 50 and 100 per cent of stock A food there was a high survival rate, resulting in 43 and 39 normal post-larvae, after 40 days. In all the populations receiving food containing less than 50 per cent of stock A, the proportion of normal post-larvae was much lower.

Table 6 The relationship between the percentage of the original number of prawn larvae (100) which successfully metamorphosed and the proportion of stock A *Artemia* in the diet

% of stock A *Artemia* in the food	% metamorphosis
0	1
5	13
10	9
20	14
50	43
100	39

LONG-TERM REARING

There has been little work as yet on the factors influencing the growth and survival of post-larvae. A population of *Palaemon serratus* has, however, been reared from the egg to nearly 200 days old under standard conditions at 20°C. At the same time a population of *P. elegans* (=*Leander squilla*) was also reared to the same stage, so giving an opportunity of comparing growth and survival in the two species. To each population, which initially contained about 150 newly-hatched larvae, fresh mussel on the shell was added after metamorphosis to supplement the diet of *Artemia*, and about a month later the *Artemia* was discontinued. In Figure 21 is shown the increase in length of the two species over this period; up to about 50 days there was no discernible difference in their growth rates, but after this *P. serratus* grew at a progressively faster rate than *P. elegans*.

Further information on the growth of the *P. serratus* population is shown in Figure 22, in which the growth rate is expressed as the increase in wet weight. After the animals were 80 days old this measure was obtained by weighing them directly; before this, weight was calculated from length observations by the previously obtained length/weight relationship shown in Figure 6. Percentage survival is also included in Figure 22. Over 154 days, the mean wet weight increased from 0.24 mg to 900 mg, and survival decreased to 13 per cent.

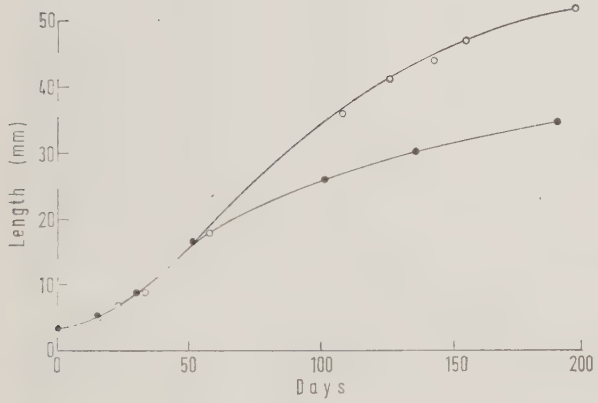


Figure 21 The growth in length of *Palaemon serratus* (open circles) and *Palaemon elegans* (solid circles) for a period of nearly 200 days from hatching.

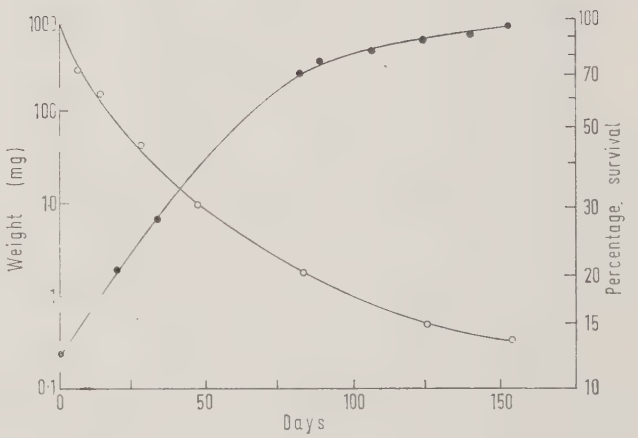


Figure 22 The growth in weight and the percentage survival of *P. serratus*.

DISCUSSION ON GROWTH AND SURVIVAL

River Conway estuary water varies very much in the quantities of particulate matter suspended in it; the nature of the material ranges from living plankton and dead marine detritus to domestic sewage and industrial effluent. Prawn larvae survival experiments with untreated water were conducted throughout one winter, and an overall decrease of 5.3 per cent per week in the survival rate occurred compared with that in filtered and irradiated water. There is no reason to suppose, however, that this figure has any real significance as a mean value over a whole year. From the point of view of the prawn larvae, the quality of the untreated water is likely to vary; it may be that at times when the estuary is rich in zooplankton larval survival in the laboratory might be enhanced by the addition of this natural food to the diet.

It is not clear why larvae in total darkness survived less well than those subjected to indirect natural lighting. Certainly their chromatophore pigments were poorly developed, and this may have reflected a more subtle biochemical deficiency. According to Goodwin (1960) knowledge of the synthesis, metabolism and function of crustacean pigments is very slight at present. Templeman (1936) found that lobster larvae grew faster and survived better in the dark, but his light-adapted animals were subject to a small amount of direct sunlight. Kurata (1962) was unable to find a differential effect between light- and dark-adapted *Cambaroides* larvae and juvenile *Porcellio*.

Agitation by bubbling air, which it was hoped might increase survival by preventing larvae from congregating, caused progressively lower growth and survival rates. It is possible that actual physical damage was being sustained by the larvae, and also that the turbulence may have interfered with their feeding mechanism. Gentle bubbling had little adverse effect, and in high densities of larvae would be essential in order to maintain an adequate oxygen concentration and to remove ammonia and carbon dioxide. The experiments described here were at larval densities low enough to avoid significant oxygen depletion.

The factors which influence the relationship between growth rate and temperature are such that it is not possible to obtain a single figure for maximum growth rate for the species, and the temperature required to obtain it. In the first place different broods of larvae have markedly different growth rates at one and the same temperature. Also, different broods show varying responses to temperature over the optimum range (Figure 15). It is clear that the average optimum temperature for growth and survival lies between 22 and 26°C (Figure 12). This suggests the possibility of selectively breeding animals which are not only the fastest growing but which also need the lowest temperature for their fastest growth rate. In this way, the minimum expenditure of energy in heating the water will be required per unit of prawn production. A further point brought out by Figure 12 is that it is not unreasonable to expect a survival of over 40 per cent in a population over the period from the newly-hatched larva to the post-larva.

According to Forster (1951a), in the wild state the first hatching of the season takes place in May, and then the first post-larvae appear in July, which suggests a period of approximately two months from hatching to metamorphosis, during which the sea temperature was probably rising to about 15°C. Under these conditions larvae were growing at perhaps half their maximum rate as determined by laboratory experiments.

Prawns which grew more slowly under the influence of reduced temperatures also passed through their larval stages more slowly; there was a basic slowing-down of their metabolism, which was manifested in both growth rate and moulting frequency. Variations in the rate of growth and duration of larval stages with temperature have been demonstrated by Costlow *et al.* (1960) and Costlow and Bookhout (1962) for various crabs, by Kurata (1962) for *Cyprinotus*, and by Templeman (1936) for *Homarus*.

Palaemon serratus lives close inshore and it is therefore not surprising that the animal possesses a wide salinity tolerance, and that fluctuations of ±40 per cent of normal salinity have little effect on larval survival. It was shown in respect of the temperature series of experiments that, although larvae were growing at different rates, the lengths at which metamorphosis occurred at different temperatures corresponded closely. In the case of salinity variations, this would not appear to be the case, unless total length was an unreliable measure of growth. It is known, for instance, that populations of *Artemia salina* reared at various salinities show marked differences in the proportions of various linear measurements (Gilchrist 1959). Possibly in the case of *Palaemon* higher salinities produce longer and thinner animals; only weight determinations could resolve this point.

As in the case of the effects of temperature, it is very likely that different broods of larvae would show slightly different responses to salinity, especially with regard to their ability to survive in very low salinities. Such attributes could be very useful in outdoor pond culture, where sudden large influxes of fresh water due to precipitation and run-off from the surrounding land are liable to occur occasionally.

Bookhout (1964), rearing the hermit crab *Pagurus*, found increases in mortalities when salinities were reduced from 35 to 15‰, and noted a slowing down of the moulting rate below 25‰. Costlow *et al.* (1960) found that *Sesarma* had an optimum salinity for each larval stage, and using statistical methods postulated the combined effects of temperature and salinity on each stage over a very wide combination of ranges of these variables. The lobster larvae of Templeman (1936) showed no variability in survival between salinities of 21 and 31‰, nor was growth affected, but below this range the survival and growth both fell off rapidly.

Parry (1954) found that the concentrations of the principal ions in the blood of the prawn were low compared with other decapods, which could be interpreted as an adaptation to estuarine conditions. Panikkar (1941) showed similar tolerances to salinity variations in adult prawns as have been reported here for larvae.

To some extent, the interrelationships between density and cannibalism have been discussed in the presentation of results. Density and survival are inversely related, though it is not clear precisely to what extent cannibalism plays a part. Late larvae and early post-larvae are known to eat early larvae, because survival of early larvae was much higher in control experiments. Larvae of the same size could be seen to seize each other, and dead larvae were rarely found despite high mortalities, but whether healthy animals were merely scavenging upon dead or dying prawns of the same size, or cannibalizing those which otherwise could have developed further, could not directly be decided. An indication is provided, however, in the extremely high survival rate of isolated larvae, where 90 per cent achieved metamorphosis successfully. It is interesting to note that in the larvae from a single brood even those which were at a density of 100/litre achieved a 67 per cent survival rate, which may be compared with the much lower figure obtained in the experiment using larvae from several broods. In the latter experiment there was also a much wider range of sizes at the end of the larval life. It has been shown that where the spread of sizes is greater the likelihood of cannibalism is also higher. As an extreme case, in a mixed population of post-larvae and newly-hatched larvae, the latter would be systematically preyed upon to extinction within a very few days.

At the higher larval densities, despite the higher mortalities shown in Figure 17, the actual production of biomass per unit of experimental culture volume was much higher than in the lower densities. Assuming the average wet weight of a late larva to be 4 mg, the production of biomass per litre at the lowest density was 10 mg, whereas at the highest density it was 431 mg (the wet weight of a newly-hatched larva is about 0.2 mg). If the supply of newly-hatched larvae in a large-scale rearing operation is not limiting, it would seem preferable to work at very high rearing densities, in order to reduce the demands on available space.

Hudinaga and Miyamura (1962) quoted figures for survival rates of *Penaeus japonicus* in mass culture which indicated that the percentage of nauplii surviving to post-larvae ranged between 5 and 17 per cent; the density of rearing was not given by these authors.

Of the various foods offered to prawn larvae, the live nauplii of the brine shrimp *Artemia* proved by far the most successful. It may well be that some of the other foods were capable of satisfying the larvae's requirements nutritionally, but, either for reasons of size, or because these foods tended to decompose quickly in sea water, larval survival was adversely affected. The food-gathering mechanism of the larvae is not adapted to filtering off suspensions of algae (see Sollaud 1923), although they did ingest large aggregations of dried *Chlorella:* no benefit, however, was derived from this food. Brine shrimp have become the standard food for rearing crustacean larvae in most larval life-history studies and were a principal component of the food mixtures offered in mass-rearing techniques for *Macrobrachium* by Ling (1962) and for *Penaeus* by Hudinaga and Miyamura (1962). Plaice larvae are also reared on this food (Shelbourne *et al.* 1963).

Although both early and late prawn larvae survived better on small (0.5 mm) *Artemia* nauplii than on fresh mussel flesh, the opposite was the case with older post-larvae; these obviously found it increasingly difficult to catch enough *Artemia* to satisfy their needs. It was found, however, in one experiment in which larvae and *Artemia* were reared together in the same bin in algal-enriched water containing no other food,

that these larvae survived and metamorphosed successfully; the few *Artemia* remaining at the end of the experiment had grown from 0.5 to 2.0 mm. It may therefore be that by adjusting the initial ratio of prawn larvae to *Artemia* a semi-automatic culture could be maintained in which the much-enlarged brine shrimp could be providing food for prawn post-larvae several weeks old.

A definite relationship was found between survival and growth and the concentration of food in the medium (Figure 19). However, too much reliance must not be placed on the figures as absolute values. The feeding levels related to initial concentrations which were made up daily, and during the 24 hours these concentrations fell at a rate which depended on the vessel volume and the number of larvae. In a rearing regime in which these various factors were different, or in which the food was continuously added to maintain a constant concentration, the level of feeding calculated to achieve maximum growth and survival might be somewhat different.

The chance discovery that different stocks of *Artemia* nauplii could variously affect the growth and survival of prawn larvae is of great importance to future large-scale rearing programmes. So far, nothing is known of the biochemical differences between the two types of *Artemia* used. During the course of this study, however, the agents supplying stock A changed their own supplier, and began to sell eggs which were claimed to originate from Utah. These eggs, while exhibiting the physical properties of stock B, nevertheless resembled stock A in respect of their food value. So it appears that the differences between the *Artemia* do not depend solely on their region of origin. It was suggested to me that stock B might be carrying a micro-organism harmful to prawn larvae, or be toxic for some other reason, such as the presence of pesticides. Purely on the meagre evidence so far available, it would also appear possible that stock B lacked or contained insufficient quantities of a trace element, vitamin or other compound vital to successful metamorphosis in prawns. If enough of stock A was available, this situation was remedied; even when it was provided only in the latter half of larval life, metamorphosis was successful. Perhaps stock B originated from a batch which were shed by parent *Artemia* at a time when their own diet lacked this unknown factor. Future studies may either isolate the factor, so that B-type stocks can be supplemented with it when given as food, or show that a few days of growth by *Artemia* fed on suitable algae will redress the deficiency. On the other hand, if the *Artemia* eggs were shown to contain toxic substances they would probably have to be completely rejected. This subject was discussed at the fifth conference on Marine Biology, Princeton, 1967 (published by the New York Academy of Sciences).

According to Cole (1958) prawns from the North Wales coast reached a length of approximately 3.5 cm at the end of the first growing season and 6.5 to 7.0 cm by October of the second season. The laboratory population reached 5.2 cm in $6\frac{1}{2}$ months (Figure 21). From the above information, a North Wales coast population would require 12–15 months to reach this size, and so would young prawns along the south coast of England, except in particularly warm years (Forster 1951a, 1959). From the work of Höglund (1943), it can be seen that similar relative figures apply to the relationship between the growth of *Palaemon elegans* in the laboratory and in the field. By rearing these species continuously at 20°C, a particular length has been obtained within no more than half the time required in the natural environment. The data in Figure 21 were obtained during the period July–January, which indicates that there is no intrinsic barrier to obtaining continued fast growth in the laboratory, even at a time when under natural conditions growth has completely ceased. For both species of *Palaemon* the temperature of the environment, rather than any rigid internal rhythm, would appear to be the controlling factor. The slower growth rate of *Palaemon elegans* in the laboratory (Figure 21A) confirms ecological studies (Forster 1951a and b) and an assumption, made at the beginning of this research, that this species is less suitable for rearing and cultivation than *P. serratus*.

Two further quantitative observations which bear upon artificial rearing are worth noting. First, a survival of 12.5 per cent over 154 days was obtained (Figure 21B), which may be compared with 5–17 per cent for the late post-larvae of *Penaeus japonicus* (Hudinaga and Miyamura 1962), although the latter would be no more than 35 days old at the time. Secondly, the total production of new tissue (expressed as wet weight) per hundred newly-hatched larvae over 154 days, taking mortality into account, was 11.23 g.

It has been pointed out above that there are wide variations between broods in their growth and survival under a particular set of conditions. The overall mean percentage of newly-hatched larvae which successfully metamorphosed during the whole course of this work was in the region of 35–45 per cent, and this

was achieved in 23–28 days at 22°C. In large-scale mass-rearing experiments these figures are not likely to be realized initially, partly due to the lack of efficient dispersion of larvae, and partly due to the presence of a range of sizes of larvae; both of these factors, as noted before, would tend to increase cannibalism. As techniques progress, it should become feasible to rear and breed animals to obtain particular genetic qualities of fast growth rate, high survival, low cannibalistic tendencies, low optimum temperature, good resistance to disease, and other attributes which may not yet be apparent. It has already been shown that a survival of 90 per cent through metamorphosis, which occurred within 20 days, is attainable (Figure 18).

Of the other published studies concerning crustacean larvae, only two were concerned with mass rearing with a view to culturing the animals up to marketable size (Ling 1962, with *Macrobrachium*, and Hudinaga and Miyamura 1962, with *Penaeus*). It is useful to compare the potentials of these species with those of *Palaemon* (see Table 7). The fecundity of the foreign animals is very much higher than that of *Palaemon*, although the survival rate in *Penaeus* is somewhat less. Ling gives no survival rate data for *Macrobrachium*. The marketable size (10 g) is very much less in *Palaemon*, and in the sea it would require at least 24 months to reach it; twelve months is an estimated time within which it might attain this weight under controlled cultivation. A 10 g prawn would be the largest marketable size for which the highest price is obtainable, although smaller animals would also find a market. The figures in Table 7 suggest that it might be useful to consider the importation of these fast-growing foreign prawn species of high fecundity, although it might prove difficult to adapt them to culture conditions in this country.

Table 7 A comparison between the approximate fecundity, marketable weight and time required to reach this size, for *Macrobrachium rosenbergi*, *Palaemon serratus* and *Penaeus japonicus*

	Fecundity (no. eggs/female)	Marketable weight (g)	Time required to reach marketable weight (months)
Macrobrachium	100 000	100	9
Palaemon	4 000	10	24 (12?)
Penaeus	400 000	25	12

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